For Reference

NOT TO BE TAKEN FROM THIS ROOM

# THE RELATIONS OF STOMATAL SIZE AND GENERATION TO THE YIELDING ABILITY OF BULKED WHEAT HYBRIDS.

B. Charles Jenkins

Department of Field Crops.

University of Alberta.

Ex Libris
Universitatis
Albertaensis

Digitized by the Internet Archive
in 2018 with funding from
University of Alberta Libraries

https://archive.org/details/relationsofstoma00char

# THE RELATIONS OF STOMATAL SIZE AND GENERATION TO THE YIELDING ABILITY OF BULKED WHEAT HYBRIDS

B. Charles Jenkins
Department of Field Crops.

A THESIS
submitted to the University of Alberta in partial fulfilment of the requirements for the degree of
MASTER OF SCIENCE
This thesis represents more than one-half of the total work.

Edmonton, Alberta
April, 1944.

Thesis
1944
#13

# TABLE OF CONTENTS.

Page

General Introduction ..... 1

Part I

The relation between stomatal size and yield in bulked wheat hybrids.

Introduction ..... 2

Literature Review ..... 4

Material and Methods ..... 8

Material ..... 8

Methods ..... 10

Tests of $F_1$ Material ..... 10

Test 1 ..... 11

Test 2 ..... 17

Test 3 ..... 17

Test of $F_2$ Material ..... 18

Experimental Results ..... 20

Tests of $F_1$ Material ..... 20

Results of Individual Tests ..... 21

Test 1 ..... 21

Test 2 ..... 21

Test 3 ..... 21

Interrelationships ..... 26

Seedling and flag leaf stomatal size relationship ..... 26

Stomatal size and yield relationships ... 30

Number of seeds, main culm ..... 30

Total seed yield ..... 33

Test of $F_2$ Material ..... 33

Selection of strains on the basis of stomatal size ..... 38

TABLE OF CONTENTS (cont'd).

Page

Stomatal size - yield test ..... 38

Selection within parental varieties ..... 39

Discussion ..... 40

Summary ..... 43

Part II

The relation between generation and yield in bulked wheat hybrids.

Introduction ..... 45

Literature Review ..... 46

Material and Methods ..... 49

Experimental results ..... 51

Summaries of bulk hybrid yield tests ..... 51

Comparison of the 1942 and 1943 results ..... 51

Heterosis in single and multiple hybrid populations 59

Yield ..... 59

Earliness ..... 80

Combining ability of parents ..... 81

Discussion ..... 84

Summary ..... 88

General Discussion ..... 90

Acknowledgements ..... 93

References ..... 94

Appendix "A"

Aids to the measurement of stomata.

I. An improved microscope slide ..... 97

II. A rapid method of identifying collected leaves .. 99

TABLE OF CONTENTS (cont'd).

Page

Appendix "B"

Tests of stage and position ..... 101

Appendix "C"

A mass crossing test ..... 107

# THE RELATIONS OF STOMATAL SIZE AND GENERATION TO THE YIELDING ABILITY OF BULKED WHEAT HYBRIDS

B. Charles Jenkins

## GENERAL INTRODUCTION

Yield in plants is an exceedingly complex character, and is the ultimate expression of the interaction of many environmental and inherent factors integrated throughout the life of the plant. It is well established that different varieties are capable of giving different yields and it is equally well established that environmental conditions play a large part in determining yield.

In crop improvement studies, yield is frequently the most important of desired characters and perhaps the most difficult to analyze. Rod-row tests are unquestionably important and necessary in the determination and final selection of a superior yielding strain, but unfortunately they are costly, time consuming and unwieldy when the number of strains is large. Any method which could be used efficiently to reduce hybrid populations in relatively early generations would be a valuable aid to the plant breeder. It was hoped that the investigations described in this thesis might suggest two methods of this nature.

The relations of stomatal size and generation to the yielding ability of bulked wheat hybrids are treated in two parts. Part I has to do with stomatal size and yield while Part II deals with generation and yield.

# PART I.

## The Relation Between Stomatal Size and Yield in Bulked Wheat Hybrids.

## INTRODUCTION.

The limiting effect of drought on crop production in western Canada has long been recognized. Little in the way of breeding resistant varieties of wheat has been accomplished, since the complex nature of drought resistance is difficult to relate to some easily recognizable character. Drought resistance possessed by any group of plants is due to a multiplicity of morphological and physiological characteristics and is further complicated by the existence of two types of drought. One, and perhaps the best known, is called "soil drought" and exists when the soil does not provide the plant with sufficient moisture to replace the amount lost by transpiration. The other, known as "atmospheric drought", is caused by hot dry winds bringing about a desiccation of the plant, even possibly under conditions of relatively high soil moisture. Plants resistant to one type of drought may not necessarily be resistant to the other.

Many phases of the drought resistance problem have been investigated with the hope of obtaining some relatively simple and practical index for determining drought resistance. This department has expended considerable time and effort in the production of drought resistant wheats - using high grain yield as the criterion by which a variety's ability to resist drought is judged, but at the same time endeavouring to refine the methods of selection so as to reduce the time and cost of producing such new varieties. It was with this latter point in mind that the present study was undertaken, following the "lead" established by previous workers in this department (2, 6, 24).

On the basis of the relationship between stomatal size and yield established by Birdsall (2), this study was undertaken to determine whether high yielding segregates or strains in a bulk population might be selected on the basis of stomatal size, i.e. length. If such a method could be used, the number of hybrid lines which would reach extensive yield tests would be materially reduced, allowing for a much more efficient program with a minimum of cost.

## LITERATURE REVIEW.

Much of the literature concerning drought resistance and methods of selecting for drought resistance, has already been reviewed extensively (1, 2, 6, 24). No attempt is made to cover in this review all this literature.

Maximov (21) regards the following anatomical peculiarities as characteristic of xerophytes: a decrease in the size of all cells, including the stomata; a thickening of the cell walls; a strong development of palisade mesophyll; a denser network of veins; and an increase in the number of stomata per unit leaf area. Most workers have agreed that these characters are associated with drought resistance.

Torrie (33) studied the genetics of several qualitative and quantitative characters in wheat as part of the drought breeding program initiated at the University of Alberta in 1929 (1). It was hoped that certain of these characters might be related to drought resistance. Aamodt and Johnston (1) undertook preliminary investigations to ascertain the resistance of wheat varieties to drought and to study in detail certain morphologic and physiologic characters associated with drought resistance and reported several interesting relations.

A preliminary study of stomatal frequency per unit leaf area in wheat varieties was made, and varietal differences established by Peto (24) in 1936. Birdsall (2) continued the work with stomatal frequency and in addition measured the length of stomata, relating both of these characters to yield and protein

content. Significant varietal differences in stomatal length and frequency were established. He found that a negative relation existed between stomatal length and yield, and a positive relation between stomatal length and protein content. Since stomatal length was found to be less variable and more accurately measured than stomatal frequency, he concluded that such a character might be more valuable for selection purposes.

Darroch (6) concluded that seedling leaf stomatal length shows some promise for the selection of high yielding types, on the basis that the seedling leaf characters are largely predetermined by embryonic development. He concluded that flag leaf stomatal length, being greatly influenced by environment, has no selection value.

Working from the viewpoint of Maximov (21) that the only true criterion of drought resistance is the ability of the plant to endure drought without injury, Platt and Darroch (25) have suggested that artificial drought tests would be useful in eliminating low yielding lines or hybrid populations. Further work by Darroch (6) emphasizes the simplicity of the soil drought survival method. The equipment necessary is available in any greenhouse. A large number of plants may be handled without much work, and the positive relation between survival and yield suggests that by using this method of selection the yield level of any population might be raised. The soil drought method has, however, certain disadvantages. There appears to be a tendency to select late maturing plants in which case the method becomes a device for eliminating the earlier maturing lines.

In an exploratory study Hopkins (17) was able to demonstrate significant effects of moisture supply on number, height, and weight of shoots, number of fertile heads and weight, size, and nitrogen content of grain per plant and per shoot of two wheat varieties. These results were obtained under winter greenhouse conditions, and may not be duplicated in all respects in the field. It was inferred, however, that observations of this type, under field plot conditions, of a relatively small number of plants grown under controlled moisture supply, might provide useful information respecting the adaptability of different varieties of plants, and the morphological aspect of drought resistance in general.

Haber (9) made a study to determine whether there were any physical or anatomical characters possessed by pure lines of corn which could be associated with resistance or susceptibility to drought and high temperature. This study was analagous to the present investigation, since, if successful, the method would be used to select resistant hybrids. It was found, however, that none of the anatomical or physical properties studied, including transpiration, number of stomata, root system and vascular bundles, provided a means of classifying unknown pure lines or strains as resistant or susceptible. A point of particular significance is that no real differences in relation to the numbers of stomata on either the upper or lower surface of the leaves could be established for resistant and susceptible lines. While numbers of stomata may not be as satisfactory as stomatal length as a criterion of drought resistance (2), the two characters have much in common.

Whiteside (35) using measurements of height, length of leaf blades, length of sheath and distance between nodes, has shown that the check gave higher measurements for each of these characters than did the plants exposed to drought. He also found that the number of veins in wheat was not less but that their distance apart was definitely less for the plants exposed to drought as compared with the checks.

## MATERIAL AND METHODS.

### Material.

Many crosses have been made in the various wheat breeding programs of the Department of Field Crops. The object has been to produce new varieties of superior merit and not necessarily for the sake of plant breeding studies. Varieties have not, therefore, been combined with other varieties in any degree of completeness.

For this study the seven varieties listed in Table I were chosen as parents. Particular attention was given to variations in stomatal size (length), yielding ability and maturity.

TABLE I

Parental Varieties.

| Variety | N. | S. | N.* |
|---|---|---|---|
| Canus .. .. .. .. | S | 34 | 1 |
| Comet .. .. .. .. | I | 36 | 3 |
| Erythrospermum 0341. .. .. | I | 36 | 74 |
| Lutescens 062 .. .. .. .. | I | 28 | 23 |
| Red Bobs .. .. .. .. | I | 0 | 18 |
| Reward .. .. .. .. | I | 35 | 5 |
| Thatcher .. .. .. .. | I | 35 | 9 |

*University of Alberta Nursery Stock Number.

For brevity and convenience in subsequent discussion the N. S. N. will not be given, Erythrospermum 0341 will be referred to as Erythro and the 062 will be dropped from Lutescens.

Canus, Red Bobs, Reward and Thatcher are well known varieties now being grown commercially in western Canada, although Reward, owing to its poor yielding ability is decreasing in importance. Comet originated as a result of a cross between Marquis and Hard Federation and is reputed to be drought resistant, early, and high yielding (5). In drought tests conducted by the Department of Field Crops, Erythro and Lutescens, two varieties of Russian origin, have given good comparative yields.* Both of these varieties are late.

In the summer of 1941 these seven varieties were crossed in all possible combinations excluding reciprocals, a total of twenty-one crosses. As far as possible, those varieties with recognizable recessive characters were chosen as female parents so that "selfs" could be eliminated in the $F_1$ generation. The method employed in making the crosses, which involves the bagging of emasculated spikes, is described by Hayes and Immer (16). A minimum of 100 seeds was obtained from all but three of the crosses. In these, however, over 95 seeds were obtained. Despite the fact that several of the combinations had previously been made in connection with the drought breeding program, they were repeated to obtain comparable material.

---

*Annual reports, Department of Field Crops, University of Alberta, 1937 - 1939 inclusive.

## Methods.

### Tests of $F_1$ Material.

Individual plants were studied in three tests made up of twenty-one $F_1$ crosses together with the seven parental varieties. Two of these tests were grown in the greenhouse and the third in the field. They will be referred to as :

Test 1 (Greenhouse - fall 1941)

Test 2 (Greenhouse - spring 1942)

Test 3 (Field - summer 1942)

Each was arranged in a randomized block design, and despite differences in replication, etc., which are mentioned later, these tests were basically similar.

Stomata were measured on seedling (first) and flag (terminal) leaves in each test. The technique and equipment used in measuring stomata has been described by Birdsall (2), and was used throughout the present investigation with the following modifications.

An improved slide and a rapid method of identifying collected leaves, described in Appendix A, were used. Instead of taking a trans-leaf sample from the base of the leaf, all measurements of stomata were made in the mid-leaf region. Supporting evidence for the value of this procedure is given in Appendix B. All measurements were made in as short a time as possible to minimize the error. Usually one "batch" was measured at a sitting. In the case of seedling leaves a "batch" consisted of one leaf from each of the twenty-eight

varieties in a replicate. For flag leaves, however, it was made up of leaves from plants at similar stages of development.

Seedling leaves were taken for stomatal measurements when the plants were in the third-leaf stage. Flag leaves were removed when the head was about two inches out of the "boot". (See Appendix B).

When the plants were mature, height and number of tillers were recorded. The number of poorly developed tillers was also noted. The main culm was not considered to be a tiller. The number of culms per plant, therefore, would be the number of tillers plus one. This system was used by Rosenquist in a study of hybrid vigor in wheat (28). Plants known to be "selfs" were discarded. Individual plant identity was maintained by placing the heads of each plant in an envelope, and to identify the head from the main culm about two inches of the stem was left attached. With the exception of Test 1, after the heads were thoroughly dry they were threshed and the following notes recorded: number of seeds in the main culm, weight of seed from the main culm and total seed weight. The latter includes all tillers.

Details of individual tests varied slightly, and these differences are dealt with in the following sections.

Test 1.

This test, seeded September 13th, 1941, was arranged in twelve replicates, each replicate being made up of three plants. For ten of the replicates (1-10) the plants were spaced in the form of an equilateral triangle, in six inch

Figure 1.

Microscope equipped for measuring stomata.

unglazed flower pots and were located on the middle bench of the greenhouse. The other two replicates (11-12) were on a side bench and the plants were not in pots. Soil to a depth of eight inches made a continuous bed, allowing for the seeds to be planted in rows. Plants were spaced two inches each way. Extra material was planted around the margins of the test to reduce "border effect". A border row of plants, potted in the same manner as the test plants, completely surrounded the material on the centre bench and also helped to reduce "border effect". Pots with weak or missing plants were moved to replicates 9 and 10 and for the purposes of recording data these were discarded, leaving ten complete replicates.

Test 1 was partly of an exploratory nature. Twenty stomata were measured for the seedling leaf of every plant in the test. It was decided, however, that for future measurements ten stomata per leaf would provide an adequate sample.

Owing to the limited amount of time available, it was only possible to measure stomata on plant number 2 for flag leaf determinations. Accordingly, the entire flag leaf was removed from number 2 plants and measurements taken. At harvest time, however, it was noted that in practically every case where the flag leaf had been removed, the seed was poorly developed. (See figures 2, 3, and 4). Growing conditions in the greenhouse in fall and winter of the year are, at best, unfavorable. Artificial light was supplied but it is impossible to approach natural conditions. Since the removal of the flag

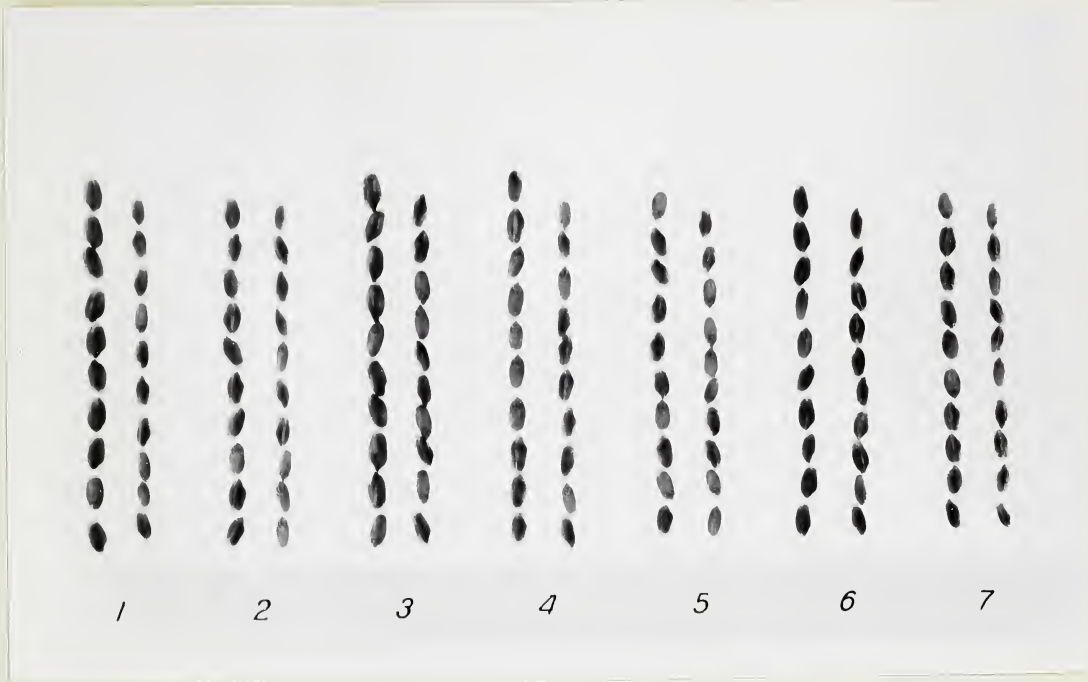



Figure 2.

The effect of flag leaf removal
on seed development of parental varieties.
(Normal - left, abnormal - right)

---

1. Canus
2. Comet
3. Erythro
4. Lutescens
5. Red Bobs
6. Reward
7. Thatcher

Figure 3.

Typical spikes (above) and seeds (below) from plants in one pot showing the effect of flag leaf removal from the No. 2 plant (centre). Plants are the $F_1$ of a cross between Lutescens and Reward.

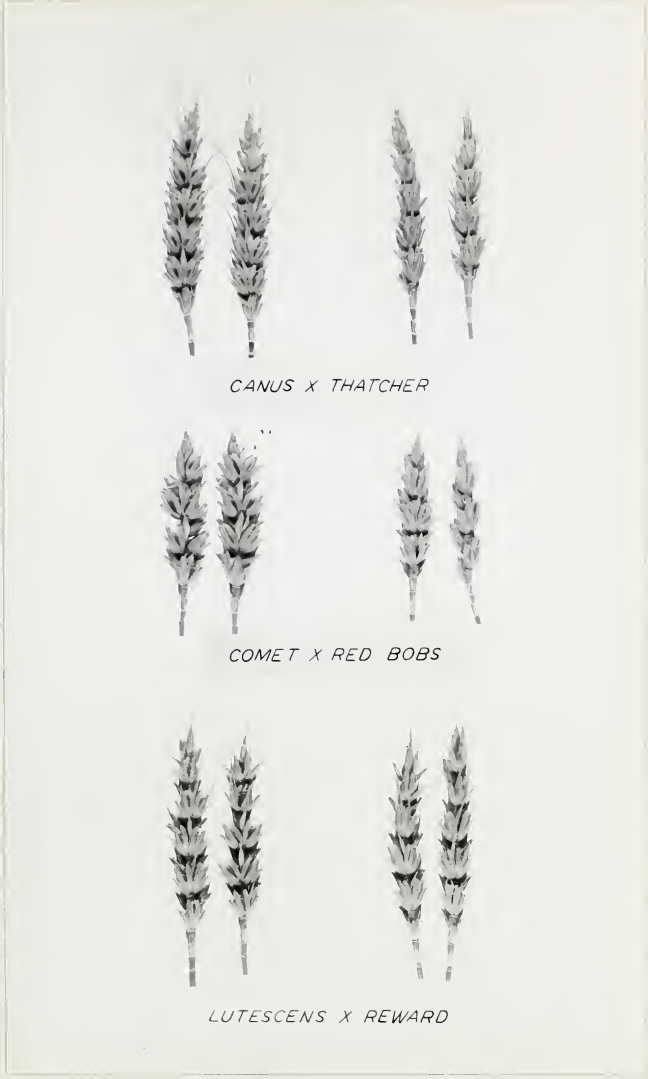



Figure 4.

The effect of flag leaf removal (right) on the appearance of spikes of $F_1$ hybrids.

leaf brought about variable degrees of shrivelling in the seed of number 2 plant, yields were recorded on the basis of number of seeds per plant rather than weight of seed per plant.

Test 2.

This test was seeded January 1st, 1942 and consisted of ten replicates, two of which acted as "border material". Pots with weak or missing plants were moved to the border, leaving eight full replicates for the test. The number of seeds per pot and their arrangement in the pots was the same as for Test 1. In this test, however, six inch glazed pots were used. Stomatal measurements, ten to each leaf, were made on all seedling and flag leaves.

Growing conditions were decidedly more favorable than for Test 1. Only half of each flag leaf was removed for stomatal measurements and no detrimental effect on seed development was noticed.

Test 3.

Test 3 was seeded in the field on May 14th, 1942. The soil was quite dry so in order to avoid possible uneven germination, the entire test was thoroughly watered on the following day. There were four replicates of single-row plots. A plot consisted of seven seeds spaced two inches apart in the row with three seeds of Dakold fall rye at each end of the row. Rows were two feet long and one foot apart. Extra rye kernels were planted to fill any blank spaces after emergence.

The planting of rye reduced "border effect" to a minimum. Three foot pathways between "banks" allowed easy access to the plants. Ten stomata per leaf were measured for all seedling and flag leaves.

Test of $F_2$ Material.

Sufficient seed was obtained from Test 3 to permit the carrying out in 1943 of a field rod-row test of the $F_2$ generation. To be consistent with the nomenclature of tests conducted by the department, this test was called the "Special $F_2$ Wheat Test". It will subsequently be referred to as the "Special $F_2$".

This test, consisting of thirty-six varieties, was arranged in a square lattice design (16). ($F_2$ hybrid populations are referred to as varieties). Seeding was done April 30th, 1943. The two-row plots were eighteen and a half feet long, with a nine inch space between rows and an eighteen-inch space between plots. The space between plots allowed for greater ease of handling, with little danger of mixing the unselected bulk populations, and at the same time afforded relatively accurate yield comparisons (14).

On the basis of the stomatal size average for both seedling and flag leaves of the parental varieties, with the exception of Reward (of which there was insufficient seed), seed of the plants was separated into "large" and "small". Only seed from those plants with the extremes in stomatal size was used, but to provide sufficient seed, approximately two thirds of the plants had to be used.

To obtain the number of varieties required by the square lattice design it was necessary to include "filler" varieties, results for which were included in the analysis, but [redacted] are not reported.

Dates of heading were the only field notes taken. Owing to exceptionally vigorous growth, considerable lodging occurred in some of the varieties, thus making notes for straw strength, height and maturity unreliable. Such notes, however, would have added little to the value of this investigation.

At maturity both rows of a plot were trimmed to sixteen and a half feet and harvested, and the four replicates of one variety were stooked together to minimize the danger of mixtures. When dry the sheaves were threshed in a small rod-row thresher and the yields recorded. Every precaution was taken to avoid mixing and loss of seed. Since the sheaves were large, the error from the loss of a small quantity of seed was reduced. Yields were calculated on the basis of three rows instead of two, thus facilitating the calculation of yield per acre.

## EXPERIMENTAL RESULTS.

### Tests of $F_1$ Material.

Table II is presented to summarize the number of recordings which make up the averages for various characters reported for Tests 1, 2 and 3. Figures in Table II represent the possible number of recordings. The actual number was not always equal to that shown, owing to "selfs" and missing values due to other causes. All missing values disappeared in replicate averages.

TABLE II

Number of Recordings Making Up the Results for Various Characters Reported for Tests 1, 2 and 3.

| | Test Number | | |
|---|---|---|---|
| | 1 | 2 | 3 |
| Stomatal Size: | | | |
| Seedling Leaf | 200 | 240 | 280 |
| Flag Leaf | 100 | 240 | 280 |
| Yield: | | | |
| Grams per plant | - | 24 | 28 |
| Seed Count (main culm) | 30 | 24 | 28 |
| Seed Weight (main culm) | - | 24 | 28 |
| Number of Tillers: | 30 | 24 | 28 |
| Height (inches): | 30 | 24 | 4 |
| Days to Heading: | 10 | 24 | - |

Results of Individual Tests.

Test 1.

The results obtained for various characters in Test 1 are reported in Table III and results of the analyses of variance for some of these in Table VI. Since the measurements of stomata on flag leaves were limited to the number 2 plants, the seedling leaf measurements reported are also limited to these plants. The lack of tillers and the low number of seeds on the main culm are indicative of the unfavorable conditions which prevailed throughout the entire period of the test.

Test 2.

Much better yields were obtained in this test than in Test 1, indicating more favorable growing conditions. A summary of the results obtained is presented in Table IV. Results of the analyses of variance for most of the characters appear in Table VI.

Test 3.

Owing to an abundant supply of moisture and the space provided for tillering, plants in this test were vigorous and productive. Slight lodging occurred just prior to maturity, but it did not affect the yield.

The results obtained for various characters in Test 3 are summarized in Table V. Results of the analysis of variance for some of the characters appear in Table VI.

In all three tests of $F_1$ material, definite varietal differences occurred for all of the characters studied. The design of these tests prohibited a multiple analysis of variance,

TABLE III

Summary of Results - Test I.
(Greenhouse, fall 1941)

| | Stomatal Size* | | Seed Count | No. of | Height in | Days to |
|---|---|---|---|---|---|---|
| | Seedling | Flag | (main culm) | tillers | ins. | heading |
| Canus | 75.7 | 60.2 | 10.6 | 0.39 | 32.2 | 74.0 |
| Comet | 79.5 | 63.1 | 11.8 | 0.04 | 27.0 | 67.0 |
| Erythro | 78.0 | 62.1 | 8.2 | 0.07 | 34.4 | 76.0 |
| Lutescens | 76.8 | 63.4 | 9.7 | 0.18 | 35.2 | 79.0 |
| Red Bobs | 77.0 | 56.0 | 13.3 | 0.00 | 32.0 | 69.5 |
| Reward | 79.8 | 63.3 | 6.6 | 0.36 | 29.4 | 64.0 |
| Thatcher | 82.7 | 65.0 | 13.3 | 0.11 | 29.0 | 66.0 |
| Canus x Comet | 80.4 | 62.0 | 13.2 | 0.04 | 29.7 | 72.0 |
| Canus x Erythro | 78.5 | 62.1 | 11.9 | 0.00 | 33.6 | 74.0 |
| Canus x Lutescens | 78.4 | 62.9 | 11.4 | 0.50 | 34.3 | 77.0 |
| Canus x Red Bobs | 78.8 | 59.6 | 11.7 | 0.00 | 32.5 | 70.5 |
| Canus x Reward | 81.0 | 62.6 | 9.0 | 0.04 | 31.4 | 69.0 |
| Canus x Thatcher | 79.9 | 62.1 | 14.4 | 0.11 | 30.8 | 69.5 |
| Erythro x Comet | 80.2 | 64.8 | 13.7 | 0.07 | 31.3 | 69.0 |
| Erythro x Lutescens | 78.4 | 63.7 | 13.0 | 0.18 | 35.8 | 74.0 |
| Erythro x Red Bobs | 76.9 | 61.0 | 13.2 | 0.00 | 33.8 | 70.5 |
| Erythro x Reward | 79.0 | 64.2 | 8.6 | 0.25 | 32.7 | 68.0 |
| Erythro x Thatcher | 82.6 | 64.5 | 11.3 | 0.14 | 31.6 | 68.5 |
| Thatcher x Comet | 80.7 | 64.1 | 11.7 | 0.11 | 29.2 | 68.5 |
| Thatcher x Lutescens | 83.0 | 65.3 | 16.5 | 0.14 | 34.5 | 70.0 |
| Thatcher x Red Bobs | 81.1 | 62.3 | 12.4 | 0.00 | 30.7 | 70.0 |
| Thatcher x Reward | 79.6 | 64.7 | 7.1 | 0.18 | 28.3 | 65.5 |
| Lutescens x Comet | 80.3 | 63.2 | 14.2 | 0.04 | 31.7 | 70.5 |
| Lutescens x Red Bobs | 75.9 | 61.4 | 14.8 | 0.00 | 34.1 | 72.0 |
| Lutescens x Reward | 79.5 | 66.6 | 13.1 | 0.00 | 33.2 | 69.0 |
| Comet x Red Bobs | 77.0 | 62.4 | 13.2 | 0.04 | 29.2 | 68.0 |
| Comet x Reward | 81.9 | 64.3 | 11.9 | 0.04 | 29.0 | 65.5 |
| Red Bobs x Reward | 79.9 | 61.3 | 9.9 | 0.07 | 29.9 | 67.0 |
| General mean | 79.4 | 62.8 | 11.8 | 0.11 | 31.7 | 70.1 |
| Min. sig. diff. | 2.8 | 2.7 | 3.0 | - | 1.8 | - |

*Stomatal size reported in micrometer scale units:
1 scale unit = 1.053 microns (2).

TABLE IV

Summary of Results - Test 2.
(Greenhouse, spring 1942)

| | Stomatal Size | | Total | Main Culm | | No. | Ht. | Days |
|---|---|---|---|---|---|---|---|---|
| | Seedling | Flag | Seed Wt.(gms.) | Seed Count | Seed Wt. | of Tillers | in ins. | to Head. |
| Canus | 81.7 | 59.3 | 1.72 | 30.6 | 1.15 | 1.4 | 35.4 | 69.0 |
| Comet | 84.6 | 61.3 | 1.57 | 21.5 | 0.95 | 1.9 | 31.4 | 66.0 |
| Erythro | 81.6 | 62.3 | 1.36 | 23.5 | 0.96 | 1.6 | 39.4 | 71.0 |
| Lutescens | 86.8 | 68.7 | 1.84 | 29.7 | 1.20 | 1.6 | 40.1 | 75.0 |
| Red Bobs | 78.6 | 56.8 | 1.25 | 22.0 | 0.86 | 2.1 | 32.6 | 66.0 |
| Reward | 85.2 | 61.3 | 0.57 | 9.0 | 0.32 | 2.6 | 27.8 | 60.5 |
| Thatcher | 86.8 | 63.0 | 1.21 | 21.9 | 0.70 | 2.0 | 30.1 | 64.0 |
| Canus x Comet | 84.9 | 60.8 | 1.89 | 26.6 | 1.10 | 1.3 | 33.5 | 69.0 |
| Canus x Erythro | 83.9 | 60.8 | 1.50 | 28.4 | 1.11 | 1.6 | 38.2 | 69.5 |
| Canus x Lutescens | 86.5 | 63.7 | 1.81 | 32.5 | 1.31 | 1.4 | 38.2 | 72.0 |
| Canus x Red Bobs | 84.0 | 58.9 | 1.45 | 23.1 | 0.94 | 1.8 | 34.1 | 69.0 |
| Canus x Reward | 87.2 | 59.4 | 1.09 | 21.1 | 0.70 | 2.1 | 31.5 | 65.0 |
| Canus x Thatcher | 85.9 | 60.5 | 1.37 | 24.3 | 0.85 | 1.8 | 33.4 | 67.5 |
| Erythro x Comet | 84.7 | 61.2 | 1.64 | 24.5 | 1.03 | 1.8 | 34.0 | 69.0 |
| Erythro x Lutescens | 86.2 | 63.4 | 2.10 | 30.8 | 1.32 | 1.6 | 40.6 | 70.5 |
| Erythro x Red Bobs | 83.6 | 58.7 | 1.61 | 22.5 | 0.96 | 1.6 | 35.9 | 66.5 |
| Erythro x Reward | 85.5 | 58.6 | 0.85 | 16.6 | 0.65 | 2.2 | 33.0 | 64.0 |
| Erythro x Thatcher | 84.1 | 60.9 | 1.16 | 20.8 | 0.81 | 2.2 | 34.6 | 65.0 |
| Thatcher x Comet | 86.3 | 62.0 | 1.34 | 21.6 | 0.79 | 1.7 | 32.4 | 65.5 |
| Thatcher x Lutescens | 88.1 | 62.0 | 1.72 | 27.9 | 1.06 | 1.4 | 36.1 | 68.5 |
| Thatcher x Red Bobs | 83.6 | 60.6 | 1.56 | 25.1 | 0.94 | 1.5 | 34.1 | 67.0 |
| Thatcher x Reward | 88.3 | 61.3 | 0.72 | 13.1 | 0.49 | 2.4 | 30.4 | 61.5 |
| Lutescens x Comet | 87.4 | 61.0 | 1.88 | 24.8 | 1.09 | 1.8 | 34.1 | 70.0 |
| Lutescens x Red Bobs | 83.9 | 59.3 | 1.91 | 30.3 | 1.28 | 1.1 | 39.0 | 69.5 |
| Lutescens x Reward | 86.7 | 62.3 | 1.33 | 21.3 | 0.87 | 2.0 | 35.1 | 67.5 |
| Comet x Red Bobs | 83.3 | 58.9 | 1.46 | 19.4 | 0.77 | 1.9 | 29.8 | 64.5 |
| Comet x Reward | 87.3 | 59.8 | 1.27 | 17.3 | 0.65 | 2.1 | 29.8 | 62.5 |
| Red Bobs x Reward | 85.0 | 59.1 | 1.21 | 19.8 | 0.75 | 2.0 | 31.8 | 64.5 |
| General mean | 85.1 | 61.0 | 1.44 | 23.2 | 0.91 | 1.8 | 34.2 | 67.1 |
| Min. sig. diff. | 2.7 | 2.0 | 0.42 | 6.5 | 0.18 | - | 2.0 | - |

TABLE V

Summary of Results - Test 3.
(Field 1942)

| | Stomatal Seedling | Size Flag | Total Seed Wt.(gms.) | Main Culm Seed Count | Main Culm Seed Wt. | No. of Tillers | Ht. in ins. |
|---|---|---|---|---|---|---|---|
| Canus | 73.3 | 65.4 | 12.77 | 51.0 | 2.14 | 6.5 | 45.2 |
| Comet | 78.2 | 65.5 | 11.23 | 39.3 | 1.82 | 6.0 | 39.5 |
| Erythro | 80.9 | 68.2 | 13.31 | 48.5 | 2.18 | 7.0 | 48.0 |
| Lutescens | 77.2 | 67.0 | 14.36 | 54.5 | 2.12 | 8.5 | 50.8 |
| Red Bobs | 74.8 | 61.6 | 12.04 | 46.3 | 1.99 | 5.8 | 45.8 |
| Reward | 78.9 | 68.4 | 6.83 | 34.3 | 1.39 | 4.5 | 44.5 |
| Thatcher | 82.2 | 67.8 | 9.91 | 46.5 | 1.79 | 5.5 | 42.0 |
| Canus x Comet | 76.9 | 65.9 | 12.56 | 49.3 | 2.15 | 6.5 | 44.5 |
| Canus x Erythro | 78.6 | 65.3 | 15.18 | 53.8 | 2.45 | 6.8 | 48.2 |
| Canus x Lutescens | 78.5 | 66.5 | 17.32 | 50.3 | 2.18 | 8.5 | 49.8 |
| Canus x Red Bobs | 78.2 | 63.2 | 11.57 | 52.3 | 2.18 | 5.5 | 47.8 |
| Canus x Reward | 81.0 | 66.2 | 10.99 | 48.5 | 2.07 | 5.5 | 47.2 |
| Canus x Thatcher | 77.3 | 68.4 | 10.58 | 49.3 | 1.97 | 5.2 | 45.2 |
| Erythro x Comet | 80.3 | 67.3 | 15.30 | 49.8 | 2.38 | 7.2 | 46.2 |
| Erythro x Lutescens | 78.3 | 68.2 | 20.82 | 55.8 | 2.65 | 10.2 | 52.2 |
| Erythro x Red Bobs | 79.5 | 65.2 | 14.83 | 52.3 | 2.40 | 7.2 | 48.8 |
| Erythro x Reward | 78.9 | 69.4 | 13.29 | 46.3 | 2.17 | 6.0 | 49.2 |
| Erythro x Thatcher | 82.0 | 69.6 | 13.63 | 47.3 | 2.14 | 7.0 | 46.2 |
| Thatcher x Comet | 82.5 | 67.4 | 9.86 | 43.5 | 1.93 | 6.0 | 43.5 |
| Thatcher x Lutescens | 82.5 | 69.0 | 14.71 | 50.3 | 2.32 | 6.8 | 49.2 |
| Thatcher x Red Bobs | 78.6 | 66.4 | 10.36 | 51.5 | 2.12 | 5.5 | 45.8 |
| Thatcher x Reward | 80.9 | 69.5 | 7.45 | 35.8 | 1.49 | 4.5 | 43.8 |
| Lutescens x Comet | 79.5 | 67.0 | 15.08 | 47.8 | 2.22 | 7.5 | 48.2 |
| Lutescens x Red Bobs | 79.5 | 63.8 | 15.83 | 53.5 | 2.25 | 7.8 | 49.5 |
| Lutescens x Reward | 80.9 | 68.7 | 12.19 | 49.5 | 2.19 | 5.8 | 50.0 |
| Comet x Red Bobs | 78.1 | 62.9 | 12.06 | 46.8 | 2.12 | 5.8 | 43.0 |
| Comet x Reward | 81.3 | 67.2 | 9.59 | 38.8 | 1.77 | 5.2 | 44.0 |
| Red Bobs x Reward | 80.5 | 65.9 | 10.91 | 42.0 | 1.83 | 6.5 | 46.2 |
| General mean | 79.2 | 66.7 | 12.66 | 47.6 | 2.08 | 6.4 | 46.6 |
| Min. sig. diff. | 3.6 | 1.3 | 2.90 | 4.3 | 0.20 | - | 1.8 |

TABLE VI

Results of the Analyses of Variance for Various Characters in Tests 1, 2 & 3.

| Variance due to : | D.F. | Mean Squares: Stomatal Size — Seedling Leaf | Stomatal Size — Flag Leaf | Total Seed Wt. | Main Culm — Seed Count | Main Culm — Seed Wt. | Height |
|---|---|---|---|---|---|---|---|
| TEST 1 | | | | | | | |
| Varieties | 27 | 39.65** | 43.60** | - | 56.00** | - | 53.4** |
| Replicates | 9 | 34.79** | 9.17** | - | 74.44** | - | 376.2** |
| Error | 243 | 11.28 | 9.05 | - | 8.28 | - | 4.2 |
| Total | 279 | | | | | | |
| TEST 2 | | | | | | | |
| Varieties | 27 | 37.87** | 38.95** | 1.0794** | 234.69** | 0.4678** | 91.9** |
| Replicates | 7 | 11.50** | 11.68** | 1.1363** | 47.63** | 0.2179** | 41.1** |
| Error | 189 | 7.26 | 4.12 | 0.1759 | 41.85 | 0.0326 | 3.8 |
| Total | 223 | | | | | | |
| TEST 3 | | | | | | | |
| Varieties | 27 | 16.68** | 16.99** | 35.0909** | 121.34** | 0.2068** | 34.0** |
| Replicates | 3 | 27.93** | 0.05 | 6.3382** | 37.03** | 0.0378 | 5.9** |
| Error | 81 | 6.34 | 0.85 | 4.1949 | 9.19 | 0.0190 | 1.6 |
| Total | 111 | | | | | | |

* Significant beyond the 5% point.

** Significant beyond the 1% point.

but in spite of a possible variety x test interaction, the varieties arranged themselves generally in the same relative order. Red Bobs consistently had small stomata while Reward, and some crosses involving it (notably Thatcher x Reward) always gave poor yields. Tillering in the greenhouse was hardly parallel to tillering in the field. In the greenhouse, in Test 2 in particular, the early varieties produced the most tillers - a definite reflection of greenhouse conditions. For the most part, however, it was considered that these three tests of $F_1$ material, and more particularly Tests 2 and 3, gave results which approach true varietal differences.

Interrelationships.

Seedling and Flag Leaf Stomatal Size Relationships.

The stomatal size results for varieties in individual tests, for both seedling and flag leaves, were simply averaged to get the results presented in Table VII. Analyses of variance (Table VIII) indicated highly significant varietal differences for both seedling and flag leaves and, as might be expected, highly significant differences for tests. The varieties and hybrids are arranged in Table VII in order of increasing stomatal size.

Although there is some similarity in the order in which varieties and hybrids arrange themselves for seedling and flag leaf stomatal size, there are striking exceptions. Erythro and Lutescens have much larger flag than seedling leaf stomata, while those crosses in which Reward is the male parent have smaller flag than seedling leaf stomata. The reason

TABLE VII

Summaries Showing Mean Seedling and Flag Leaf Stomatal Size Results for Tests 1, 2 & 3.

| Seedling | | Flag | |
|---|---|---|---|
| Red Bobs | 76.8 | Red Bobs | 58.1 |
| Canus | 76.9 | Canus x Red Bobs | 60.6 |
| Comet x Red Bobs | 79.5 | Comet x Red Bobs | 61.4 |
| Lutescens x Red Bobs | 79.8 | Lutescens x Red Bobs | 61.5 |
| Erythro x Red Bobs | 80.0 | Canus | 61.6 |
| Erythro | 80.2 | Erythro x Red Bobs | 61.6 |
| Lutescens | 80.3 | Red Bobs x Reward | 62.1 |
| Canus x Erythro | 80.3 | Canus x Reward | 62.4 |
| Canus x Red Bobs | 80.3 | Canus x Erythro | 62.7 |
| Canus x Comet | 80.7 | Canus x Comet | 62.9 |
| Comet | 80.8 | Thatcher x Red Bobs | 63.1 |
| Canus x Thatcher | 81.0 | Comet | 63.3 |
| Erythro x Lutescens | 81.0 | Canus x Thatcher | 63.3 |
| Canus x Lutescens | 81.1 | Lutescens x Comet | 63.7 |
| Thatcher x Red Bobs | 81.1 | Comet x Reward | 63.8 |
| Erythro x Reward | 81.2 | Erythro x Reward | 64.1 |
| Reward | 81.3 | Erythro | 64.2 |
| Erythro x Comet | 81.7 | Canus x Lutescens | 64.3 |
| Red Bobs x Reward | 81.8 | Erythro x Comet | 64.4 |
| Lutescens x Comet | 82.3 | Thatcher x Comet | 64.5 |
| Lutescens x Reward | 82.4 | Reward | 64.7 |
| Erythro x Thatcher | 82.9 | Erythro x Thatcher | 65.0 |
| Thatcher x Reward | 82.9 | Thatcher x Reward | 65.2 |
| Canus x Reward | 83.1 | Thatcher | 65.3 |
| Thatcher x Comet | 83.2 | Erythro x Lutescens | 65.4 |
| Comet x Reward | 83.5 | Thatcher x Lutescens | 65.4 |
| Thatcher | 83.9 | Lutescens x Reward | 65.9 |
| Thatcher x Lutescens | 84.5 | Lutescens | 66.4 |
| General mean | 81.2 | | 63.5 |
| Min. sig. diff. | 2.2 | | 2.2 |

| | | | |
|---|---|---|---|
| | | | |
| | | | |
| | | | |

for this difference is without explanation unless environment has been largely responsible. Darroch (6) has shown conclusively that environment may affect stomatal size in flag leaves. It should be remembered, however, that Erythro and Lutescens are late varieties and that the crosses with Reward as the male parent are, for the most part, early.

Despite these minor discrepancies, a highly significant correlation coefficient of 0.672 between seedling leaf stomatal size and flag leaf stomatal size was obtained. The results correlated are those presented in Table VII and represent the average of all three tests (720 individual measurements for seedling leaves and 620 for flag leaves). The correlation surface is shown in Figure 5. Positions of parental varieties are indicated. The relationship existing between stomatal size on seedling and flag leaves for this material is far better than the one found by Darroch (6) but is still far from perfect, indicating environmental or other influence.

TABLE VIII

Results of the Analyses of Variance for Seedling and Flag Leaf Stomatal Size Averages for Tests 1, 2, and 3.

| Variance due to: | D. F. | Mean Squares | |
|---|---|---|---|
| | | Seedling | Flag |
| Variety | 27 | 9.85** | 9.88** |
| Test | 2 | 307.72** | 240.98** |
| Error | 54 | 1.81 | 1.83 |
| Total | 83 | | |

**Significant beyond the 1% point.

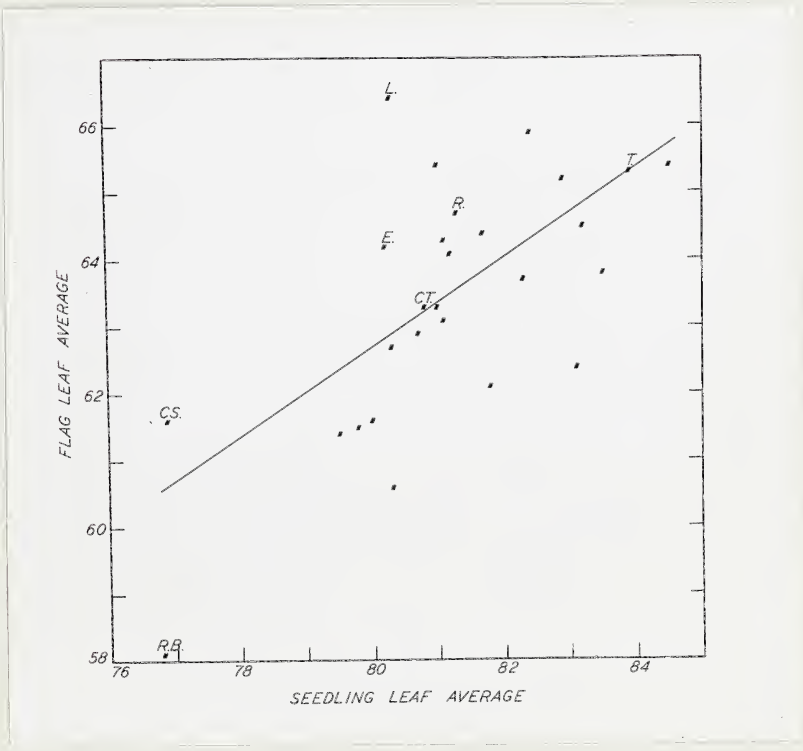



Figure 5.

Relation between seedling and flag leaf stomatal size.

Stomatal Size and Yield Relationships.

One of the main objects of the present study was to determine the extent of the relationship between stomatal size and yield. Since total seed yield was not obtainable for Test 1, the number of seeds on the main culm were taken to represent yield. Stomatal sizes for seedling and flag leaves were individually related with number of seeds on the main culm and total seed yield and are discussed in the following sections.

Number of Seeds, Main Culm.

A summary of the number of seeds, main culm, obtained in the three tests of $F_1$ material is given in Table IX. The varieties and hybrids are arranged in descending order of productivity, expressed on a percentage basis. Instead of averaging individual test results directly, they were changed to a percentage of the general mean and then averaged. In this way equal weight was given to each test.

Little relationship was found to exist between number of seeds, main culm and either seedling or flag leaf stomatal size. Insignificant correlation coefficients of -0.205 and -0.118, respectively, were obtained. The correlation surfaces in Figure 6 show the widely scattered distribution of points. Parental varieties are indicated and, had the same been done for the hybrids, they would have been seen to group themselves round the common parent.

TABLE IX

Number of Seeds on the Main Culm for Three Tests.

| | No. of Seeds, Main Culm | | | Mean* |
|---|---|---|---|---|
| | Test 1 | Test 2 | Test 3 | (% Basis) |
| Lutescens x Red Bobs | 14.8 | 30.3 | 53.5 | 122.7 |
| Thatcher x Lutescens | 16.5 | 27.9 | 50.3 | 121.8 |
| Erythro x Lutescens | 13.0 | 30.8 | 55.8 | 120.0 |
| Canus x Lutescens | 11.4 | 32.5 | 50.3 | 114.0 |
| Canus x Erythro | 11.9 | 28.4 | 53.8 | 112.0 |
| Canus x Comet | 13.2 | 26.6 | 49.3 | 110.0 |
| Canus x Thatcher | 14.4 | 24.3 | 49.3 | 110.0 |
| Canus | 10.6 | 30.6 | 51.0 | 109.5 |
| Lutescens x Comet | 14.2 | 24.8 | 47.8 | 109.1 |
| Erythro x Comet | 13.7 | 24.5 | 49.8 | 108.7 |
| Lutescens | 9.7 | 29.7 | 54.5 | 108.1 |
| Thatcher x Red Bobs | 12.4 | 25.1 | 51.5 | 107.1 |
| Erythro x Red Bobs | 13.2 | 22.5 | 52.3 | 106.2 |
| Canus x Red Bobs | 11.7 | 23.1 | 52.3 | 102.8 |
| Lutescens x Reward | 13.1 | 21.3 | 49.5 | 102.2 |
| Red Bobs | 13.3 | 22.0 | 46.3 | 101.5 |
| Thatcher | 13.3 | 21.9 | 46.5 | 101.5 |
| Comet x Red Bobs | 13.2 | 19.4 | 46.8 | 97.9 |
| Erythro x Thatcher | 11.3 | 20.8 | 47.3 | 94.9 |
| Thatcher x Comet | 11.7 | 21.6 | 43.5 | 94.5 |
| Comet | 11.8 | 21.5 | 39.3 | 91.7 |
| Erythro | 8.2 | 23.5 | 48.5 | 90.8 |
| Canus x Reward | 9.0 | 21.1 | 48.5 | 89.6 |
| Red Bobs x Reward | 9.9 | 19.8 | 42.0 | 85.7 |
| Comet x Reward | 11.9 | 17.3 | 38.8 | 85.6 |
| Erythro x Reward | 8.6 | 16.6 | 46.3 | 80.5 |
| Thatcher x Reward | 7.1 | 13.1 | 35.8 | 63.9 |
| Reward | 6.6 | 9.0 | 34.3 | 55.5 |
| General mean | 11.8 | 23.2 | 47.7 | 99.9 |
| Min. sig. diff. | 3.0 | 6.5 | 4.3 | - |

*Obtained by expressing the results for individual tests in percent of the general mean and averaging the percentage figures obtained.

[illegible]

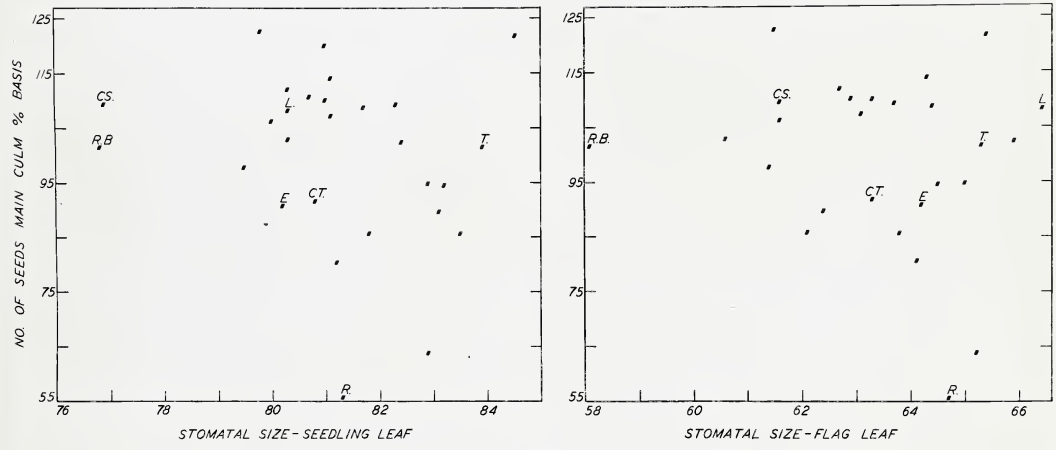



Figure 6.

Relation between the number of seeds on the main culm and stomatal size for seedling and flag leaves.

Total Seed Yield.

Large test differences made necessary the conversion of individual results to a percentage basis before averages could be obtained. In Table X are the results for total seed yield of varieties and hybrids in two of the three $F_1$ tests.

Practically no relationship was found to exist between total seed yield and stomatal size of either the seedling or flag leaves. Insignificant correlation coefficients of -0.245 and 0.002 respectively were obtained. The correlation surfaces are shown in Figure 7. Owing to variability in tillering, the range for total seed yield is much greater than for number of seeds on the main culm. These characters are, nevertheless, related. Although the results are not presented, a rough correlation surface was drawn up for the relationship of number of seeds on the main culm, and total seed yield. A scatter indicating a high correlation was obtained.

Test of $F_2$ Material.

Results for the Special $F_2$ test are presented in Table XI.

The analysis of variance for yield appears in Table XII.

In the field test, strains of parental varieties were separated on the basis of large and small stomata. For summary purposes the results obtained for these selections were simply averaged.

TABLE X

Total Seed Yield, per plant basis, for two tests.

| | Total Seed Yield (gms. per plant) | | Mean* |
|---|---|---|---|
| | Test 2 | Test 3 | (% Basis) |
| Erythro x Lutescens | 2.10 | 20.82 | 155.1 |
| Canus x Lutescens | 1.81 | 17.32 | 131.2 |
| Lutescens x Red Bobs | 1.91 | 15.83 | 128.8 |
| Lutescens x Comet | 1.88 | 15.08 | 124.8 |
| Lutescens | 1.84 | 14.36 | 120.6 |
| Thatcher x Lutescens | 1.72 | 14.71 | 117.8 |
| Erythro x Comet | 1.64 | 15.30 | 117.4 |
| Canus x Comet | 1.89 | 12.56 | 115.2 |
| Erythro x Red Bobs | 1.61 | 14.83 | 114.4 |
| Canus x Erythro | 1.50 | 15.18 | 112.0 |
| Canus | 1.72 | 12.77 | 110.2 |
| Erythro | 1.36 | 13.31 | 99.8 |
| Comet | 1.57 | 11.23 | 98.8 |
| Comet x Red Bobs | 1.46 | 12.06 | 98.4 |
| Canus x Red Bobs | 1.45 | 11.57 | 96.0 |
| Thatcher x Red Bobs | 1.56 | 10.36 | 95.0 |
| Lutescens x Reward | 1.33 | 12.19 | 94.4 |
| Erythro x Thatcher | 1.16 | 13.63 | 94.2 |
| Red Bobs | 1.25 | 12.04 | 91.0 |
| Canus x Thatcher | 1.37 | 10.58 | 89.4 |
| Thatcher x Comet | 1.34 | 9.86 | 85.4 |
| Red Bobs x Reward | 1.21 | 10.91 | 85.1 |
| Erythro x Reward | 0.85 | 13.29 | 82.0 |
| Comet x Reward | 1.27 | 9.59 | 82.0 |
| Thatcher | 1.21 | 9.91 | 81.2 |
| Canus x Reward | 1.09 | 10.99 | 81.2 |
| Thatcher x Reward | 0.72 | 7.45 | 54.4 |
| Reward | 0.57 | 6.83 | 46.8 |
| General mean | 1.44 | 12.66 | 100.1 |
| Min. sig. diff. | 0.42 | 2.90 | - |

*Obtained by expressing the results for individual tests in percent of the general mean and averaging the percentage figures obtained.

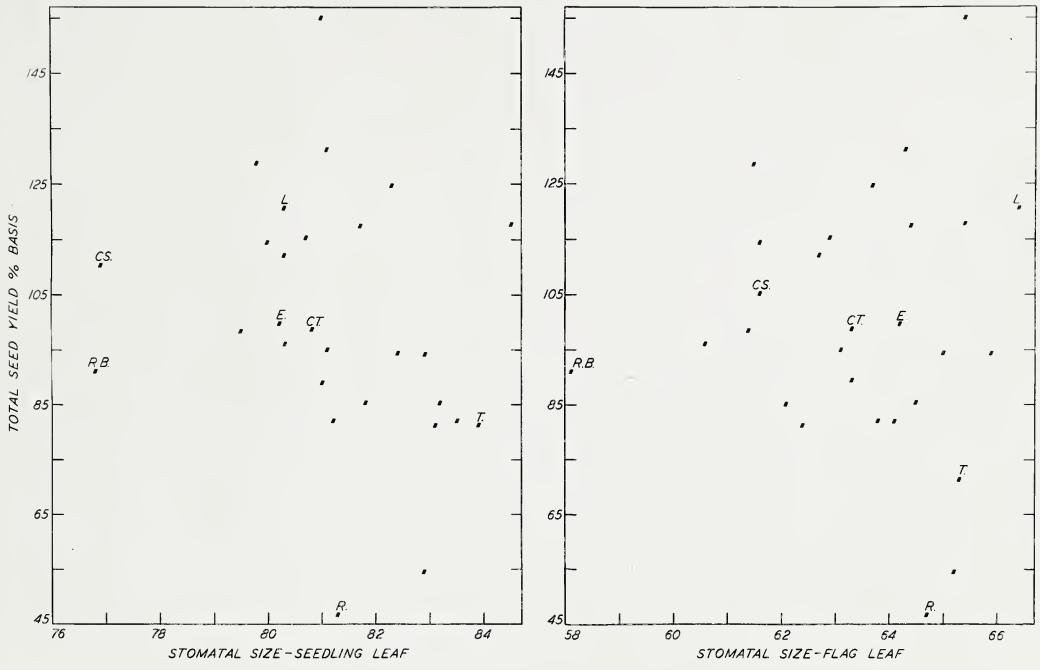



Figure 7.

Relation between total seed yield and stomatal size for seedling and flag leaves.

TABLE XI

Summary of Results - Special $F_2$ Test, 1943.

| | Yield (Bus. per ac.) | Days to Heading |
|---|---|---|
| Erythro x Comet | 74.8 | 74 |
| Thatcher x Comet | 72.8 | 72 |
| Erythro x Thatcher | 68.3 | 74 |
| Erythro x Lutescens | 67.7 | 78 |
| Lutescens x Red Bobs | 66.4 | 76 |
| Thatcher | 66.2 | 71 |
| Canus x Thatcher | 66.2 | 76 |
| Canus x Lutescens | 64.6 | 79 |
| Canus x Comet | 63.8 | 76 |
| Thatcher x Red Bobs | 63.1 | 72 |
| Comet x Reward | 63.0 | 70 |
| Canus x Reward | 62.4 | 74 |
| Thatcher x Lutescens | 62.2 | 76 |
| Erythro x Reward | 61.8 | 71 |
| Erythro x Red Bobs | 60.7 | 74 |
| Lutescens x Comet | 59.8 | 75 |
| Comet x Red Bobs | 58.8 | 71 |
| Red Bobs | 58.4 | 71 |
| Red Bobs x Reward | 58.2 | 70 |
| Thatcher x Reward | 57.7 | 70 |
| Canus x Erythro | 56.7 | 77 |
| Canus x Red Bobs | 56.2 | 74 |
| Comet | 55.6 | 72 |
| Lutescens x Reward | 53.6 | 74 |
| Reward | 52.3 | 69 |
| Erythro | 52.0 | 77 |
| Lutescens | 52.0 | 82 |
| Canus | 50.3 | 78 |
| Mean | 60.9 | 74 |
| Min. sig. diff. | 6.7 | - |

Table 2

Summary of Census Data - Counties of [illegible], 1960.

TABLE XII

Results of the Analysis of Variance
for Yield,
Special $F_2$ Test , 1943.

| Variance due to: | D. F. | M. S. | F. |
|---|---|---|---|
| Varieties | 35 | 163.14 | 6.40** |
| Replicates | 3 | 85.01 | 3.34* |
| Error | 105 | 25.49 | |
| Total | 143 | | |

* Significant beyond the 5% point.

** Significant beyond the 1% point.

Owing to rather severe lodging in the latter part of the season, the very late varieties did not fill properly. Evidence of somewhat abnormal yields for Canus, Erythro and Lutescens is shown in Table XI. Ordinarily these varieties would appear much higher in the list.

A higher but still non-significant correlation coefficient of 0.416 was obtained when seedling leaf stomatal size for $F_1$ tests was correlated with yields of parental varieties and F2 hybrid populations. In this case, however, the relationship is positive.

Selection of Strains on the basis of Stomatal Size. Stomatal Size - Yield Test.

On the assumption that higher yielding strains within a variety might be selected on the basis of stomatal size, Birdsall in 1940 made stomatal measurements on 200 plants in each of three varieties, namely Canus S-34-I, Caesium x Marquis H-37-20 and I-28-60 x Milturum H-29-35. (The two hybrids mentioned showed promise as drought resistant varieties and were at that time in advance yield tests.) Plant identity was retained, a few with the largest and a few with the smallest stomata were harvested and increased in 1941. A quadruplicated single rod-row yield test, including sixteen strains of Canus and eight strains each of H-37-20 and H-29-35, was conducted at Edmonton in 1942. This test was called the "Stomatal Size-Yield Test". The yield results appear in Table XIII. Statistical treatment of the results did not appear to be

TABLE XIII

Summary of Results, Stomatal Size - Yield Test 1942 (showing yield and stomatal size of several strains of three wheat varieties selected for large and small stomata)

| Strain | | Canus | | H-29-35 | | H-37-20 | |
|---|---|---|---|---|---|---|---|
| | | Stomatal Size* | Yield (bus. per ac.) | Stomatal Size* | Yield (bus. per ac.) | Stomatal Size* | Yield (bus. per ac.) |
| Large | 1 | 65.6 | 59.1 | 67.4 | 59.6 | 69.4 | 62.7 |
| | 2 | 65.4 | 61.1 | 68.0 | 55.3 | 69.0 | 61.4 |
| | 3 | 66.0 | 58.6 | 67.8 | 64.6 | 69.3 | 60.8 |
| | 4 | 65.1 | 61.8 | 67.5 | 62.6 | 69.1 | 62.0 |
| | 5 | 65.6 | 57.0 | | | | |
| | 6 | 66.1 | 52.1 | | | | |
| | 7 | 69.8 | 55.1 | | | | |
| | 8 | 65.6 | 54.8 | | | | |
| Mean | | 66.2 | 57.4 | 67.7 | 60.5 | 69.2 | 61.7 |
| Small | 1 | 51.3 | 58.6 | 58.3 | 60.4 | 60.2 | 58.4 |
| | 2 | 49.1 | 60.0 | 59.8 | 61.2 | 60.8 | 64.6 |
| | 3 | 54.8 | 56.4 | 58.1 | 62.2 | 60.1 | 66.7 |
| | 4 | 53.9 | 56.3 | 59.5 | 60.5 | 60.0 | 64.0 |
| | 5 | 46.2 | 56.8 | | | | |
| | 6 | 52.6 | 50.0 | | | | |
| | 7 | 54.1 | 54.1 | | | | |
| | 8 | 54.5 | 57.8 | | | | |
| Mean | | 52.1 | 56.2 | 58.9 | 61.1 | 60.3 | 63.4 |
| Difference, Large minus Small | | 14.1 | 1.2 | 8.8 | -0.6 | 8.9 | -1.7 |

*Average of 10 flag leaf stomatal measurements for single plants, 1940.

necessary to indicate the lack of difference between "large" and "small" selections.

It would appear from the results of this test that stomatal size has no selection value.

Selection Within Parental Varieties.

Plants of parent varieties in Tests 2 and 3 were separated on the basis of stomatal size. An average of stomatal measurements on seedling and flag leaves of the plants allowed a separation into "large" and "small". Seed from the "large" and "small" strains for Test 3 was used in the Special $F_2$.

Results of stomatal size and yield differences for six parental varieties appear in Table XIV. The $t$ test of significance was used to determine the significance of the difference between mean "large" and mean "small" selection yields. Despite a few individual differences in favor of "small" selections, the mean for "large" was greater in every test. The difference was significant beyond the 5% point in two of the three tests. It is reasonable to suppose that similar differences might have been found had strains of the $F_1$ hybrid material been separated on the basis of stomatal size, since $F_1$ hybrids are completely heterozygous, giving each plant the same genetic constitution. These results do not support the theory that plants with small stomata are the higher yielders. Actually it would appear that selection on the basis of small stomatal size becomes a device for obtaining small weak plants.

TABLE XIV

Stomatal Size and Yield for "within variety" selections of six wheat varieties in three yield tests.

| | Stomatal Size | | | Yield (gms. per plant) | | | t |
|---|---|---|---|---|---|---|---|
| | Large | Small | Diff. | Large | Small | Diff.+ | Value |
| Test 2. | | | | | | | |
| Canus | 72.6 | 68.6 | 4.0 | 1.73 | 1.78 | -0.05 | |
| Comet | 74.8 | 70.6 | 4.2 | 1.56 | 1.39 | 0.17 | |
| Erythro | 75.0 | 69.4 | 5.6 | 1.59 | 1.10 | 0.49 | |
| Lutescens | 80.0 | 75.5 | 4.5 | 1.88 | 1.80 | 0.08 | |
| Red Bobs | 70.2 | 65.4 | 4.8 | 1.42 | 1.15 | 0.27 | |
| Thatcher | 77.2 | 72.8 | 4.4 | 1.38 | 1.06 | 0.32 | |
| Mean | 75.0 | 70.4 | 4.6 | 1.59 | 1.38 | 0.21 | 2.73* |
| Test 3. | | | | | | | |
| Canus | 72.8 | 66.2 | 6.6 | 15.02 | 10.86 | 4.16 | |
| Comet | 75.5 | 68.4 | 7.1 | 13.29 | 9.40 | 3.89 | |
| Erythro | 75.8 | 72.8 | 3.0 | 12.53 | 13.20 | -0.67 | |
| Lutescens | 74.7 | 68.8 | 5.9 | 13.94 | 13.82 | 0,12 | |
| Red Bobs | 70.5 | 66.1 | 4.4 | 14.44 | 9.54 | 4.09 | |
| Thatcher | 78.1 | 72.6 | 5.5 | 11.83 | 8.94 | 2.89 | |
| Mean | 74.6 | 69.2 | 5.4 | 13.51 | 10.96 | 2.55 | 2.73* |
| Special $F_2$. | | | | Yield (bu./ac.) | | | |
| Canus | 72.8 | 66.2 | 6.6 | 53.5 | 47.1 | 6.4 | |
| Comet | 75.5 | 68.4 | 7.1 | 57.4 | 53.9 | 3.5 | |
| Erythro | 75.8 | 72.8 | 3.0 | 53.0 | 51.1 | 1.9 | |
| Lutescens | 74.7 | 68.8 | 5.9 | 50.8 | 53.3 | -2.5 | |
| Red Bobs | 70.5 | 66.1 | 4.4 | 59.2 | 57.6 | 1.6 | |
| Thatcher | 78.1 | 72.6 | 5.5 | 66.5 | 65.9 | 0.6 | |
| Mean | 74.6 | 69.2 | 5.4 | 56.7 | 54.8 | 1.9 | 1.56 |

+A minus sign indicates that the yield is higher for the smaller selection.

*5% point, t = 2.57.

## DISCUSSION.

According to Worzella (37) a test of relationship between characters must be simple, accurate and specific before it can be of much use in identifying and measuring accurately varietal or strain differences. The use of stomatal size (length) to determine the relative drought resistance, as measured by yield, of wheat varieties or strains has been studied in the present investigation. To be of practical value a high relationship must exist. Judged by these standards, the stomatal size yield relationship has no selection value.

With protein content, high yield is associated with low protein (22) but with stomatal size there is no standard relation which can be used as a basis for selection. Red Bobs, for example, has small stomata and gives a good yield, while Thatcher has large stomata and also yields well. While minor discrepancies do occur in the relation between protein content and yield, this relation would be much more valuable for selection purposes than the stomatal size and yield relationship.

It might be argued that a better relationship would have been found had the plants been grown under limited moisture supply (21); but even allowing for this, it is felt that the relation between stomatal size and yield would be of no practical value. At best differences are not great, and even within varieties large plant differences occur. If seedling leaf stomatal measurements were used as a basis of selection, unless the undesirable plants were immediately eliminated, an accurate method of plant identification would have to be devised. This would entail a considerable amount of work, which in addition

to the labor involved in measuring, would greatly limit the size of population to be handled. Flag leaf stomatal measurements would be easier to obtain, but environment plays a large part in determining stomatal size on these leaves. To be useful to the plant breeder, a specific test should be applicable to large populations and the stomatal size and yield relationship fails in this respect.

There seems to be little doubt that stomatal size is a varietal characteristic. Despite the association between small stomata and high yield, varieties do exist which have large stomata and yield well. It is suggested that a possible reason for the negative relation between stomatal size and yield is that there is usually a greater number of varieties with small stomata giving good yields.

Selection of plants on the basis of stomatal size has actually been studied. In contrast to what might be expected, the plants with large stomata nearly always gave higher yields, lending further support to the explanation already suggested for the negative relationship. If the idea expressed by Maximov (21), that plants with small cells have small stomata, is accepted, then it would appear that selection on the basis of small stomatal size becomes a device for accumulating small, poor yielding plants. The results of the present investigation seem to support such a theory. In an unselected bulk population, however, this may not be true since the plants selected are actually new varieties. It is unfortunate that the present material did not permit a more thorough study of unselected

hybrid populations, but in any case if stomatal size were used as a criterion for selection this character in the parents would have to be known. Little difficulty would be encountered if one parent had large stomata and gave a low yield while the other parent had small stomata and gave a high yield or if the reverse were true, but such an ideal relation seldom exists. Many varieties have medium sized stomata, some giving poor, others medium and still others high yields. The whole relationship is too complex to have any practical application in a breeding program.

Immer (19) has concluded from a study of spaced barley plants that the variation in yield of single plants in spaced progeny rows is determined almost completely by environmental factors. In the present study it was thought that the yields obtained closely approached those which might actually be expected. The plants Immer studied were spaced five inches apart in rows one foot apart, and this might account for the lack of varietal differences.

## SUMMARY.

The relation between stomatal size and yield has been studied for seven parental varieties and twenty-one $F_1$ hybrid populations. Some sixty thousand stomata were measured during the course of the investigation. All possible parental combinations except reciprocals were made. These may be considered as essentially twenty-eight varieties since the $F_1$ hybrid plants being completely heterozygous, have the same genetic constitution. Using yield per plant, as measured by the number of seeds in the main culm and total seed weight, no relationship was found to exist between it and the stomatal length for either seedling (first) or flag (terminal) leaves. Seedling leaf stomatal length was actually more closely related to yield than flag leaf stomatal length, as indicated by slightly higher correlation coefficients, but neither relation was statistically significant.

Selection on the basis of small stomatal size (length) within varieties produced no increase in the yield of the resultant strains and although further testing would be necessary to substantiate the results obtained, it would appear that this method becomes a device for selecting the poor yielding weak plants.

Despite the fact that stomatal size is a varietal characteristic, there does not appear to be any standard or "best" size which may be sought.

Owing to the complexities of the problem and the limitations imposed by the high expense and the unreliability of the relationship, it is concluded that the relation between

stomatal size and yield has no selection value.

---

## PART II

---

## The Relation Between Generation and Yield in Bulked Wheat Hybrids.

---

## INTRODUCTION

Any method which might be employed efficiently to reduce hybrid populations in early generations so as to minimize the cost of ultimate rod-row testing would be a valuable aid to the cereal plant breeder. Several workers (11,13,18) have indicated that yield tests of unselected bulk populations in early generations might be used as a basis for discarding those crosses which will eventually give only a few high-yielding segregates. In similar studies Taylor (32) attempted to evaluate bulk progenies from single and multiple crosses in wheat and barley. Although the number of progenies was large, he had the results of only one year's testing on which to base conclusions. Since Taylor's material was confined to the $F_2$ generation, except for a few hard wheat single crosses in $F_3$, comparison of generations was practically impossible.

The present study was made for the purpose of supplementing the results obtained by Taylor. The fundamental aims of these two investigations have been in most respects identical, though the scope of this study has been enlarged by the use of more than one generation and the addition of hybrid populations from all possible combinations, excluding reciprocals, of seven hard spring wheat varieties.

It was hoped that this investigation with these additions would not only corroborate the results already obtained, but would indicate more conclusively the value of various crosses as a source of future superior selections and the combining ability of parents for use in breeding programs.

## LITERATURE REVIEW

Since a great deal of the literature has already been reviewed by Taylor (32), repetition will be avoided as far as possible.

The results obtained by Harrington (13) have furnished information of value on the usefulness of bulk hybrid yield trials in evaluating crosses. He nevertheless felt that it would be worth while to have parental varieties $F_1$, $F_2$ and $F_3$ in the same replicated yield trial. In addition, he realized that a number of economic characters other than yield may be limiting factors. For such characters as milling and baking quality, disease resistance, and resistance to certain weather conditions, bulk hybrid trials would be of little value. Resistance to insect attack and more particularly resistance to wheat stem sawfly might be added to the list.

The complexities of yield have been considered by several workers (3, 4, 36, 37). In most cases, attempts have been made to separate various yield attributes in order to simplify the yield complex. It is generally considered that of the many characters present in wheat, yield is the most difficult to analyze. While the plant breeder is interested primarily in the inherent factors affecting yield, the importance of the environmental factors must not be overlooked, since they affect the physiology and morphology of the plant in a way that is directly related to yield.

Suneson and Wiebe (31) in studies with wheat and barley have suggested that the relative yield of a variety is not necessarily a criterion of its ability to survive in competition with other varieties grown in mixtures in the same locality. Barley variety mixtures were tested extensively by Harlan and Martini (10). In experiments with a mixture of eleven varieties grown for four to twelve years at ten stations, they found evidence at certain stations of early aggressiveness and increasing dominance of the local commercial type. At other points, however, the locally grown commercial variety in the mixture was depressed and varieties not grown in those localities dominated the mixture after a time. Papadakis (23) has shown that natural selection among wheat varieties sown in mixed stands does not always favor the varieties that give the higher grain yields when sown alone under the same conditions. It was concluded that high grain yield does not constitute the only factor on which depends dominance in the struggle for existence and also that wheat varieties differ in aggressiveness, each being remarkably constant in this respect.

The foregoing reports of disparity between individual and competitive yields suggest a decided limitation to the success of the bulked population method of cereal breeding. These have in addition a direct bearing on the use of yield tests of unselected bulk populations as a basis for discarding those crosses which will eventually give a low percentage of high-yielding segregates.

Harlan et al (11) have shown that certain varieties of barley are more valuable as parents than others. This is demonstrated by their ability to produce an unusually high percentage of superior segregates in their offspring while others give only a few high-yielding segregates. Some varieties which were considered to be unpromising, as judged by their performance in nursery tests, were found to be superior parents.

Taylor (32), in a study of wheat bulk hybrids, has shown that the yield of the parental varieties is a valuable indication of their combining ability. He has suggested, however, that each variety should be combined with each other variety in a more complete investigation.

## MATERIAL AND METHODS.

The material used in the present study consisted largely of the unselected bulk populations grown by Taylor (32) in 1942, and was, therefore, advanced one generation. In addition there was a residue from the seed used by Taylor.

The "early wheat hybrids", "soft wheat hybrids" and "barley hybrids" were all grown in 1943, but this discussion is limited to the results from the first two. The names of tests were altered slightly to be consistent with the nomenclature of tests conducted by the Department of Field Crops. The early wheat hybrid yield test became the "Special hybrid hard wheat test" and the soft wheat hybrid yield test became the "Special hybrid soft wheat test". The 1943 names will be used throughout the subsequent discussion.

The Special hybrid hard wheat test involved a comparison of 56 unselected bulk hard wheat hybrids and 8 parental varieties. The hybrid populations included the following groups of crosses: in the $F_2$ generation - 10 single and 2 double crosses, in the $F_3$ generation - 11 single, 6 triple, 11 double, 2 five-variety, 4 six-variety and 1 eight-variety, and in the $F_4$ generation 9 single. The terminology used in describing the crosses has been given by Taylor (32).

The Special hybrid soft wheat test involved a comparison of 43 unselected bulk wheat crosses made for the purpose of producing an early soft wheat, and 6 parental varieties. The hybrid populations included the following groups of crosses: in the $F_2$ generation - 8 single, and in the $F_3$ generation - 10 single, 11 triple and 14 double crosses.

The size and arrangement of plots, the experimental design and the method of handling described for the "Special $F_2$ Wheat Test" in Part I of this thesis applies also to both of these tests. The arrangement of plots is illustrated in Figure 8.

In addition to the hard and soft wheat crosses, the present investigation includes the consideration of some results obtained from the tests to determine the relation between stomatal size and yield in wheat hybrids. Full details of these tests appear in Part I.

Figure 8.

Partial view of Special Hybrid Tests, 1943, showing the arrangement of plots.

## EXPERIMENTAL RESULTS

### Summaries of Bulk Hybrid Yield Tests.

Results obtained for the Special hybrid hard wheat test and the Special hybrid soft wheat test are summarized in Tables XV and XVI respectively. In each table the varieties and hybrids are arranged in descending order of yield within each group. Analysis of variance for yield for varieties and hybrid populations in these tests appear in Tables XVII and XVIII.

Yields of the late varieties, notably H-37-30, H-29-35 and crosses involving these varieties, are noticeably below normal. Owing to severe lodging in the latter part of the season, varieties and hybrids such as these did not develop properly.

### Comparison of the 1942 and 1943 Results.

Since several of the parental varieties and hybrids were common to tests in 1942 (32) and 1943, it was possible to make two year comparisons. Abnormally high yields were obtained im both of these years in all tests.

The relationship between the 1942 and 1943 results was tested by correlation. For parental varieties in the hard wheat hybrid test, a non-significant correlation coefficient of 0.584 was obtained. A higher but still not significant coefficient of 0.682 was obtained for the soft wheat parental varieties. Despite the lack of significance, due to the low number of comparisons possible, there does seem to be a fair relationship between the 1942 and 1943 yields of the parental varieties. (see Figure 9).

TABLE XV
Summary of Results, Special Hybrid Hard Wheat Test, 1943.

| | Yield (bu./ac.) | Days to Heading |
|---|---|---|
| **Parental Varieties** | | |
| Red Bobs | 65.7 | 72 |
| Thatcher | 56.6 | 73 |
| H-37-30 | 54.9 | 80 |
| Canus | 54.5 | 76 |
| H-29-35 | 53.1 | 80 |
| 1515-29.27 | 50.8 | 67 |
| Reward | 50.3 | 70 |
| 482B | 35.6 | 70 |
| **Single Crosses $F_2$** | | |
| Canus x Red Bobs | 67.5 | 75 |
| Red Bobs x Reward | 62.4 | 71 |
| Canus x Thatcher | 60.4 | 75 |
| 482B x Thatcher | 59.8 | 70 |
| H-37-30 x Reward | 51.0 | 74 |
| H-37-30 x 482B | 49.4 | 71 |
| H-37-30 x Canus | 48.5 | 77 |
| H-29-35 x 482B | 47.5 | 73 |
| H-29-35 x Reward | 46.1 | 74 |
| 482B x Canus | 45.2 | 71 |
| **Single Crosses $F_3$** | | |
| Canus x Red Bobs | 63.0 | 75 |
| H-29-35 x Reward | 58.6 | 75 |
| Red Bobs x Reward | 58.1 | 70 |
| 482B x Canus | 52.0 | 71 |
| Canus x Thatcher | 50.5 | 74 |
| Red Bobs x 1515-29.27 | 50.3 | 70 |
| H-37-30 x Canus | 48.5 | 78 |
| H-37-30 x 482B | 48.3 | 72 |
| H-37-30 x Reward | 48.2 | 70 |
| 482B x Thatcher | 46.6 | 70 |
| H-29-35 x 482B | 45.0 | 73 |
| **Single Crosses $F_4$** | | |
| Canus x Red Bobs | 65.7 | 72 |
| H-29-35 x Reward | 65.0 | 74 |
| H-37-30 x Canus | 64.5 | 77 |
| Red Bobs x 1515-29.27 | 58.2 | 70 |
| Red Bobs x Reward | 57.8 | 71 |
| H-37-30 x 482B | 54.7 | 72 |
| Canus x Thatcher | 51.4 | 71 |
| H-29-35 x 482B | 50.3 | 74 |
| 482B x Canus | 44.9 | 70 |

.....continued

TABLE XV (cont'd)

| | Yield (bu./ac.) | Days to Heading |
|---|---|---|
| **Triple Crosses $F_3$** | | |
| (Red Bobs x 1515-29.27) Canus | 67.8 | 74 |
| (Canus x Red Bobs)Thatcher | 63.7 | 74 |
| (Canus x Thatcher)Red Bobs | 55.3 | 74 |
| (H-29-35 x Reward)H-37-30 | 50.4 | 77 |
| (Red Bobs x Reward)Thatcher | 46.9 | 72 |
| (H-37-30 x 482B)H-29-35 | 40.1 | 76 |
| **Double Crosses $F_2$** | | |
| (H-29-35 x Reward)(H-37-30 x 482B) | 59.2 | 73 |
| (Canus x Thatcher)(Red Bobs x 1515-29.27) | 55.3 | 72 |
| **Double Crosses $F_3$** | | |
| (H-29-35 x Reward)(H-37-30 x 482B) | 58.4 | 74 |
| (Canus x Thatcher)(Red Bobs x 1515-29.27) | 56.9 | 71 |
| (Red Bobs x 1515-29.27)(H-37-30 x Canus) | 56.1 | 71 |
| (Red Bobs x 1515-29.27)(H-37-30 x Reward) | 54.5 | 71 |
| (482B x Thatcher)(H-37-30 x Reward) | 53.8 | 73 |
| (Canus x Thatcher)(Red Bobs x Reward) | 51.4 | 74 |
| (482B x Thatcher)(H-37-30 x Canus) | 51.0 | 73 |
| (Canus x Thatcher)(H-37-30 x 482B) | 50.6 | 74 |
| (482B x Thatcher)(H-29-35 x Reward) | 50.6 | 72 |
| (482B x Canus)(Red Bobs x Reward) | 47.0 | 70 |
| (482B x Thatcher)(Red Bobs x Reward) | 41.2 | 70 |
| **Five Variety Crosses $F_3$** | | |
| (H-29-35 x Rew.)(H-37-30 x 482B)Red Bobs | 56.7 | 73 |
| (H-29-35 x Rew.)(H-37-30 x 482B)Thatcher | 50.3 | 72 |
| **Six Variety Crosses $F_3$** | | |
| [(Can.x That.)(R.B.x1515-29.27)](H-37-30xCan.) | 61.6 | 74 |
| [(Can.x That.)(R.B.x1515-29.27)](H-29-35xRew.) | 57.2 | 72 |
| [(H-29-35xRew.)(H-37-30x482B)](Can.x That.) | 53.4 | 74 |
| [(Can.x That.)(R.B.x1515-29.27)](Master x Rew.) | 53.0 | 70 |
| **Eight Variety Cross $F_3$** | | |
| [(H-29-35xRew.)(H-37-30x482B)]x[(Can.x That.)(R.B.x1515-29.27)] | 56.6 | 73 |
| General Mean | 53.7 | 73 |
| Min. Sig. Diff. | 6.4 | - |

TABLE XVI

Summary of Results, Special Hybrid Soft Wheat Test, 1943.

| | Yield (bu./ac.) | Days to Heading |
|---|---|---|
| **Parental Varieties** | | |
| Pacific Bluestem | 59.3 | 81 |
| Dicklow | 53.4 | 86 |
| Master | 52.6 | 68 |
| Onas | 48.1 | 77 |
| Prelude | 44.6 | 68 |
| 482B | 35.2 | 70 |
| **Single Crosses $F_2$** | | |
| Dicklow x Onas | 65.8 | 81 |
| Pacific Bluestem x Onas | 60.3 | 80 |
| Pacific Bluestem x Prelude | 59.4 | 72 |
| Dicklow x 482B | 56.8 | 76 |
| Onas x Prelude | 53.6 | 70 |
| Pacific Bluestem x Dicklow | 53.2 | 83 |
| Onas x 482B | 45.7 | 72 |
| Pacific Bluestem x 482B | 44.1 | 75 |
| **Single Crosses $F_3$** | | |
| Dicklow x Onas | 57.4 | 80 |
| Pacific Bluestem x Onas | 57.4 | 78 |
| Pacific Bluestem x Prelude | 56.3 | 75 |
| Onas x Prelude | 52.7 | 71 |
| Pacific Bluestem x Dicklow | 51.1 | 82 |
| 482B x Master | 50.3 | 68 |
| Dicklow x 482B | 49.0 | 76 |
| Onas x 482B | 46.9 | 72 |
| Pacific Bluestem x 482B | 44.7 | 74 |
| Master x Prelude | 40.2 | 68 |
| **Triple Crosses $F_3$** | | |
| (P.B.S. x Onas)482B | 58.6 | 74 |
| (Dicklow x 482B)482B | 54.2 | 73 |
| (Dicklow x Onas)Prelude | 53.7 | 73 |
| (P.B.S. x Onas)Prelude | 51.1 | 72 |
| (Dicklow x 482B)Dicklow | 50.4 | 80 |
| (Dicklow x Onas)Master | 50.1 | 74 |
| (P.B.S. x Dicklow)Master | 49.8 | 75 |
| (P.B.S. x Onas)Master | 48.8 | 73 |
| (Onas x Prelude)Master | 44.1 | 69 |
| (P.B.S. x 482B)Master | 43.2 | 71 |
| (P.B.S. x Dicklow)Prelude | 43.1 | 74 |

....continued

TABLE XVI (cont'd)

| Double Crosses $F_3$ | Yield (bu./ac.) | Days to Heading |
|---|---|---|
| (Dicklow x Onas)(Master x Prelude) | 62.1 | 73 |
| (Dicklow x 482B)(P.B.S. x Onas) | 57.6 | 77 |
| (482B x Master)(Dicklow x Onas) | 56.3 | 74 |
| (Onas x 482B)(P.B.S. x Prelude) | 53.3 | 74 |
| (482B x Master)(P.B.S. x Dicklow) | 52.9 | 75 |
| (Onas x Prelude)(P.B.S. x 482B) | 52.1 | 74 |
| (Onas x 482B)(Onas x Prelude) | 51.1 | 71 |
| (P.B.S. x Prelude)(Dicklow x 482B) | 50.2 | 75 |
| (Onas x Prelude)(Dicklow x 482B) | 50.0 | 75 |
| (P.B.S. x 482B)(Onas x Prelude) | 49.9 | 73 |
| (Dicklow x 482B)(Onas x 482B) | 48.7 | 76 |
| (P.B.S. x 482B)(Onas x 482B) | 48.7 | 74 |
| (P.B.S. x Dicklow)(Master x Prelude) | 48.4 | 75 |
| (Dicklow x Onas)(P.B.S. x 482B) | 45.7 | 76 |
| General Mean | 51.3 | 74 |
| Min. Sig. Diff. | 7.9 | - |

TABLE XVII

Results of the Analysis of Variance for Yield, Special Hybrid Hard Wheat Test 1943.

| Variance due to: | D. F. | M. S. | F. |
|---|---|---|---|
| Varieties | 63 | 180.03 | 8.63** |
| Replicates | 3 | 74.51 | 3.57* |
| Error | 189 | 20.86 | |
| TOTAL | 255 | | |

* Significant beyond the 5% point.
** Significant beyond the 1% point.

TABLE XVIII

Results of the Analysis of Variance for Yield, Special Hybrid Soft Wheat Test 1943.

| Variance due to: | D. F. | M. S. | F. |
|---|---|---|---|
| Varieties | 48 | 157.18 | 5.06** |
| Replicates | 3 | 74.55 | 2.40-- |
| Error | 144 | 31.04 | |
| TOTAL | 195 | | |

** Significant beyond the 1% point.

--

Yields for those hybrids which were in $F_2$ in 1942 and $F_3$ in 1943 were correlated for both hard and soft wheat hybrids. Variations in hybrid vigor will admittedly affect such a relationship. However, it was thought that some indication of the closeness of relation for the two years' results might be obtained. For the hard wheat hybrids, a non-significant coefficient of -0.050 was obtained, while for the soft wheat hybrids the coefficient was 0.559 and highly significant. The correlation surfaces involved are shown in Figure 10.

Field observations lend support to the statistical results obtained. Little lodging occurred in the 1942 test of hard wheat hybrids, while in 1943 lodging was severe. Variations in maturity, straw strength and height would all contribute to differential results for the two years. Lodging in the soft wheat hybrid test was equally as bad in 1942 as in 1943. This undoubtedly accounts largely for the better relationship, indicated by significant correlation coefficients.

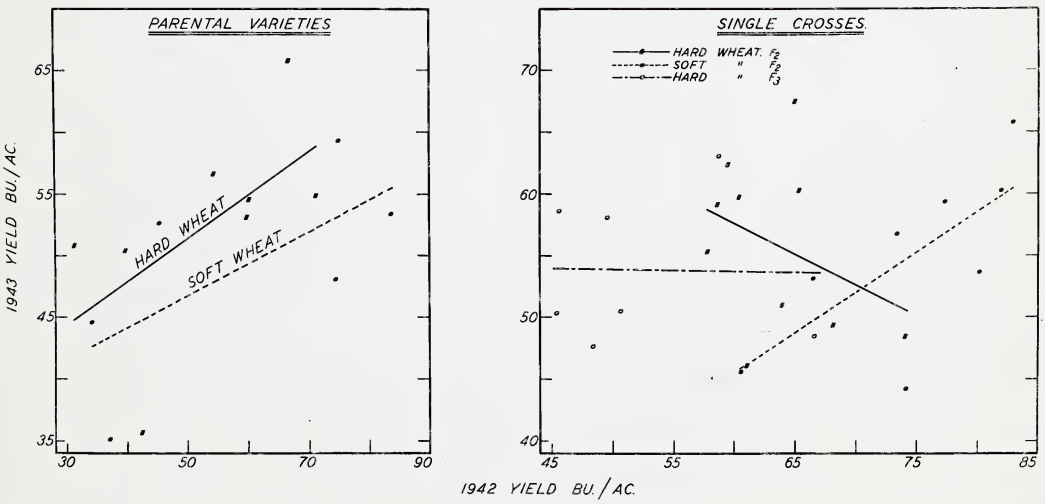



Figure 9.

Relation between the yields for 1942 and 1943 of the hard and soft wheat parental varieties and a few single crosses.

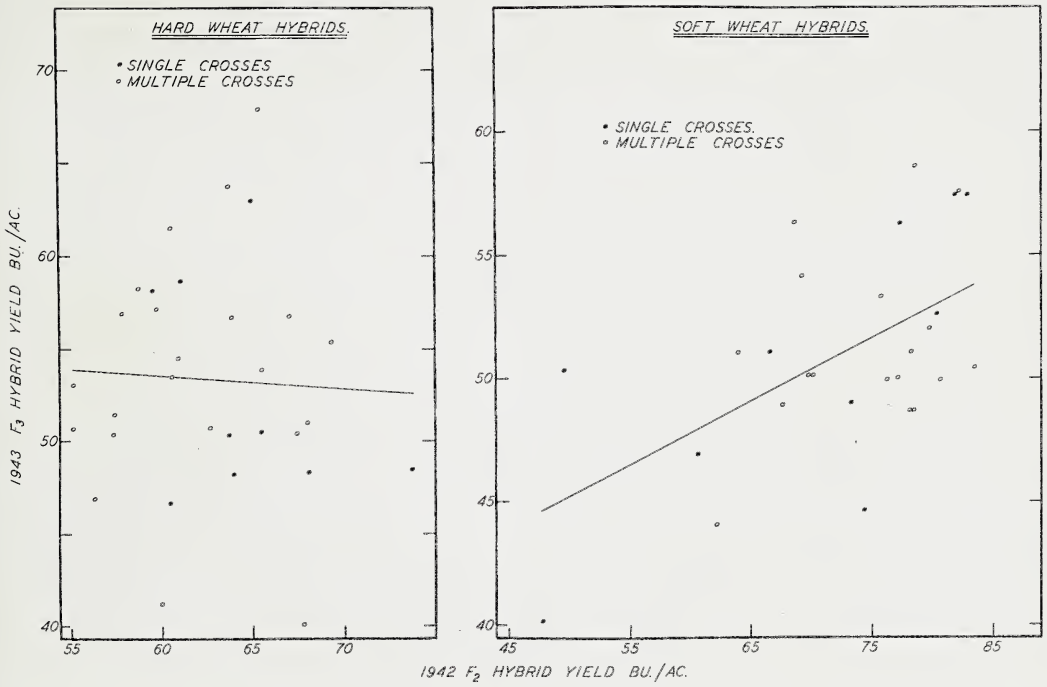



Figure 10.

Relation between the $F_2$ yields for 1942 and the $F_3$ yields for 1943 of several hard and soft wheat hybrids.

Heterosis* in Single and Multiple Hybrid Populations.

Yield.

Heterosis for yield was not so consistently demonstrated in 1943 as in 1942. Some crosses gave yields above the parental averages while almost an equal number yielded below the parental averages. Yields varied considerably but the range was not as great as in 1942.

Comparing the single crosses in the special hybrid hard wheat test, those in the $F_4$ generation showed the greatest amount of hybrid vigor, the $F_2$ next and the $F_3$ least (Table XIX). The fact that the $F_4$ hybrid yield has shown an increase above the parental average over the $F_2$ and $F_3$ is probably due to a greater predominance of high yielding segregates. The majority of the multiple hybrid populations are in the $F_3$ generation, and the absence of hybrid vigor is apparent. It is perhaps significant, however, that, of the multiple crosses, all three of those involving six varieties and the one involving eight varieties have yielded more than the parental average. The 1942 results (32) show that these crosses demonstrated no more vigor than the other multiple combinations. It may be that six and eight-variety crosses would, by intensifying the qualities of several parents in one variety, be valuable as a source of high yielding segregates.

The results in Table XX again show that single crosses in the $F_3$ generation have less vigor than those in the $F_2$. Hybrid vigor was more general for the soft wheat hybrids than for the hard wheat hybrids (cf. Tables XIX and XX).

---

*Heterosis (hybrid vigor) is considered as an increase over the average of the parents for the characters under study.

TABLE XIX

Comparisons of the $F_2$, $F_3$ and $F_4$ Yields
of Single and Multiple Hard Wheat Crosses, with the Parental Average.

| | Yield (bu./ac.) | | | $F_2$ in % of Par. Av. |
|---|---|---|---|---|
| | $F_2$ | Par. Av. | $F_2$ Min. Par. Av. | |
| Single Crosses | | | | |
| Canus x Red Bobs | 67.5 | 60.1 | 7.4 | 112 |
| Red Bobs x Reward | 62.4 | 58.0 | 4.4 | 108 |
| Canus x Thatcher | 60.4 | 55.6 | 4.8 | 109 |
| 482B x Thatcher | 59.8 | 46.1 | 13.7 | 130 |
| H-37-30 x Reward | 51.0 | 52.6 | -1.6 | 97 |
| H-37-30 x 482B | 49.4 | 45.2 | 4.2 | 109 |
| H-37-30 x Canus | 48.5 | 54.7 | -6.2 | 89 |
| H-29-35 x 482B | 47.5 | 44.4 | 3.1 | 107 |
| H-29-35 x Reward | 46.1 | 51.7 | -5.6 | 89 |
| 482B x Canus | 45.2 | 45.0 | 0.2 | 100 |
| Mean | 53.8 | 51.3 | 2.4 | 105 |
| Double Crosses | | | | |
| (H-29-35 x Reward)(H-37-30 x 482B) | 59.2 | 48.5 | 10.7 | 122 |
| (Canus x Thatcher)(Red Bobs x 1515-29.27) | 55.3 | 56.9 | -1.6 | 97 |
| Mean | 57.2 | 52.7 | 4.6 | 110 |

.... continued.

TABLE XIX (cont'd)

| | Yield (bu./ac.) | | | $F_3$ in % of |
|---|---|---|---|---|
| | $F_3$ | Par. Av. | $F_3$ Min. Par. Av. | Par. Av. |
| Single Crosses | | | | |
| Canus x Red Bobs | 63.0 | 60.1 | 2.9 | 105 |
| H-29-35 x Reward | 58.6 | 51.7 | 6.9 | 113 |
| Red Bobs x Reward | 58.1 | 58.0 | 0.1 | 100 |
| 482B x Canus | 52.0 | 45.0 | 7.0 | 116 |
| Canus x Thatcher | 50.5 | 55.6 | -5.1 | 91 |
| Red Bobs x 1515-29.27 | 50.3 | 58.2 | -7.9 | 86 |
| H-37-30 x Canus | 48.5 | 54.7 | -6.2 | 89 |
| H-37-30 x 482B | 48.3 | 45.2 | 3.1 | 107 |
| H-37-30 x Reward | 48.2 | 52.6 | -4.4 | 92 |
| 482B x Thatcher | 46.6 | 46.1 | 0.5 | 101 |
| H-29-35 x 482B | 45.0 | 44.4 | 0.6 | 101 |
| Mean | 51.7 | 52.0 | -0.2 | 100 |
| Triple Crosses. | | | | |
| (Red Bobs x 1515-29.27)Canus | 67.8 | 56.4 | 11.4 | 120 |
| (Canus x Red Bobs)Thatcher | 63.7 | 58.4 | 5.3 | 109 |
| (Canus x Thatcher)Red Bobs | 55.3 | 60.6 | -5.3 | 91 |
| (H-29-35 x Reward)H-37-30 | 50.4 | 53.3 | -2.9 | 95 |
| (Red Bobs x Reward)Thatcher | 46.9 | 57.3 | -10.4 | 82 |
| (H-37-30 x 482B)H-29-35 | 40.1 | 49.2 | -9.1 | 82 |
| Mean | 54.0 | 55.9 | -1.8 | 96 |

..... continued.

TABLE XIX (cont'd)

| | Yield (bu./ac.) | | | $F_3$ in % of Par. Av. |
|---|---|---|---|---|
| | $F_3$ | Par. Av. | $F_3$ min. Par Av. | |
| Double Crosses | | | | |
| (H-29-35 x Reward)(H-37-30 x 482B) | 58.4 | 48.5 | 9.9 | 120 |
| (Canus x Thatcher)(Red Bobs x 1515-29.27) | 56.9 | 56.9 | 0.0 | 100 |
| (Red Bobs x 1515-29.27)(H-37-30 x Canus) | 56.1 | 56.5 | -0.4 | 99 |
| (Red Bobs x 1515-29.27)(H-37-30 x Reward) | 54.5 | 55.4 | -0.9 | 98 |
| (482B x Thatcher)(H-37-30 x Reward) | 53.8 | 49.4 | 4.4 | 109 |
| (Canus x Thatcher)(Red Bobs x Reward) | 51.4 | 56.8 | -5.4 | 90 |
| (482B x Thatcher)(H-37-30 x Canus) | 51.0 | 50.4 | 0.6 | 101 |
| (Canus x Thatcher)(H-37-30 x 482B) | 50.6 | 50.4 | 0.2 | 100 |
| (482B x Thatcher)(H-29-35 x Reward) | 50.6 | 48.9 | 1.7 | 103 |
| (482B x Canus)(Red Bobs x Reward) | 47.0 | 51.5 | -4.5 | 91 |
| (482B x Thatcher)(Red Bobs x Reward) | 41.2 | 52.0 | -10.8 | 79 |
| Mean | 52.0 | 52.4 | -0.5 | 99 |
| Five-Variety Crosses | | | | |
| (H-29-35 x Rew.)(H-37-30 x 482B)Red Bobs | 56.7 | 57.0 | -0.3 | 99 |
| (H-29-35 x Rew.)(H-37-30 x 482B)Thatcher | 50.3 | 52.5 | -2.2 | 96 |
| Mean | 53.5 | 54.8 | -1.2 | 98 |
| Six-Variety Crosses | | | | |
| [Can.x That.)(R.B.x1515-29.27)](H-37-30xCan.) | 61.6 | 55.8 | 5.8 | 110 |
| [(Can.x That.)(R.B.x1515-29.27)](H-29-35 x Rew.) | 57.2 | 54.4 | 2.8 | 105 |
| [(H-29-35xRew.)(H-37-30x482B)](Can. x That.) | 53.4 | 52.0 | 1.4 | 103 |
| Mean | 56.1 | 54.1 | 3.3 | 106 |
| Eight-Variety Cross | | | | |
| [(H-29-35 x Rew.)(H-37-30x482B)]x[Can.x That.)(R.B.x1515-29.27)] | 56.6 | 52.7 | 3.9 | 107 |

.....continued.

TABLE XIX (cont'd)

| | Yield (bu./ac.) | | | $F_4$ in % of |
|---|---|---|---|---|
| | $F_4$ | Par. Av. | $F_4$ Min. Par. Av. | Par. Av. |
| Single Crosses | | | | |
| Canus x Red Bobs | 65.7 | 60.1 | 5.6 | 109 |
| H-29-35 x Reward | 65.0 | 51.7 | 13.3 | 126 |
| H-37-30 x Canus | 64.5 | 54.7 | 9.8 | 118 |
| Red Bobs x 1515-29.27 | 58.2 | 58.2 | 0.0 | 100 |
| Red Bobs x Reward | 57.8 | 58.0 | -0.2 | 100 |
| H-37-30 x 482B | 54.7 | 45.2 | 9.5 | 121 |
| Canus x Thatcher | 51.4 | 55.6 | -4.2 | 92 |
| H-29-35 x 482B | 50.3 | 44.4 | 5.9 | 113 |
| 482B x Canus | 44.9 | 45.0 | -0.1 | 100 |
| Mean | 56.9 | 52.5 | 4.4 | 109 |

TABLE XX

Comparisons of the $F_2$ and $F_3$ Yields of Single & Multiple Soft Wheat Crosses, with the Parental Average.

| | Yield (bu./ac.) | | | $F_2$ in % of Par. Av. |
|---|---|---|---|---|
| | $F_2$ | Par. Av. | $F_2$ Min. Par. Av. | |
| Single Crosses | | | | |
| Dicklow x Onas | 65.8 | 50.8 | 15.0 | 130 |
| Pacific Bluestem x Onas | 60.3 | 53.7 | 6.6 | 112 |
| Pacific Bluestem x Prelude | 59.4 | 52.0 | 7.4 | 114 |
| Dicklow x 482B | 56.8 | 44.3 | 12.5 | 128 |
| Onas x Prelude | 53.6 | 46.4 | 7.2 | 116 |
| Pacific Bluestem x Dicklow | 53.2 | 56.4 | -3.2 | 94 |
| Onas x 482B | 45.7 | 41.6 | 4.1 | 110 |
| Pacific Bluestem x 482B | 44.1 | 47.2 | -3.1 | 93 |
| Mean | 54.9 | 49.0 | 5.8 | 112 |

| | Yield (bu./ac.) | | | $F_3$ in % of Par. Av. |
|---|---|---|---|---|
| | $F_3$ | Par. Av. | $F_3$ Min. Par. Av. | |
| Single Crosses | | | | |
| Dicklow x Onas | 57.4 | 50.8 | 6.6 | 113 |
| Pacific Bluestem x Onas | 57.4 | 53.7 | 3.7 | 107 |
| Pacific Bluestem x Prelude | 56.3 | 52.0 | 4.3 | 108 |
| Onas x Prelude | 52.7 | 46.4 | 6.3 | 114 |
| Pacific Bluestem x Dicklow | 51.1 | 56.4 | -5.3 | 91 |
| 482B x Master | 50.3 | 43.9 | 6.4 | 115 |
| Dicklow x 482B | 49.0 | 44.3 | 4.7 | 111 |
| Onas x 482B | 46.9 | 41.6 | 5.3 | 113 |
| Pacific Bluestem x 482B | 44.7 | 47.2 | -2.5 | 95 |
| Master x Prelude | 40.2 | 48.6 | -8.4 | 83 |
| Mean | 50.6 | 48.5 | 2.1 | 105 |
| Triple Crosses | | | | |
| (P.B.S.xOnas)482B | 58.6 | 44.4 | 14.2 | 132 |
| (Dicklow x 482B)482B | 54.2 | 39.8 | 14.4 | 136 |
| (Dicklow x Onas)Prelude | 53.7 | 47.7 | 6.0 | 113 |
| (P.B.S.xOnas)Prelude | 51.1 | 49.2 | 1.9 | 104 |
| (Dicklow x 482B)Dicklow | 50.4 | 48.8 | 1.6 | 103 |
| (Dicklow x Onas)Master | 50.1 | 51.7 | -1.6 | 97 |
| (P.B.S.x Dicklow)Master | 49.8 | 54.5 | -4.7 | 91 |
| (P.B.S.xOnas)Master | 48.8 | 53.2 | -4.4 | 92 |
| (Onas x Prelude)Master | 44.1 | 49.5 | -5.4 | 89 |
| (P.B.S.x482B)Master | 43.2 | 49.9 | -6.7 | 87 |
| (P.B.S.x Dicklow)Prelude | 43.1 | 50.5 | -7.4 | 85 |
| Mean | 49.7 | 49.0 | 0.7 | 103 |

....continued.

TABLE XX (cont'd)

| | Yield (bu./ac.) | | | $F_3$ in % of |
|---|---|---|---|---|
| | $F_3$ | Par. Av. | $F_3$ Min. Par. Av. | Par. Av. |
| Double Crosses | | | | |
| (Dicklow x Onas)(Master x Pre.) | 62.1 | 49.7 | 12.4 | 125 |
| (Dick.x482B)(P.B.S.xOnas) | 57.6 | 49.0 | 8.6 | 118 |
| (482BxMaster)(Dick.xOnas) | 56.3 | 47.4 | 8.9 | 119 |
| (Onas x482B)(P.B.S.x Pre.) | 53.3 | 46.8 | 6.5 | 114 |
| (482BxMaster)(P.B.S.xDick.) | 52.9 | 50.2 | 2.7 | 105 |
| (Onas x Pre.)(P.B.S.x482B) | 52.1 | 46.8 | 5.3 | 111 |
| (Onas x482B)(Onas x Pre.) | 51.1 | 44.0 | 7.1 | 116 |
| (P.B.S.xPre.)(Dick.x482B) | 50.2 | 48.2 | 2.0 | 104 |
| (Onas xPre.)(Dick.x482B) | 50.0 | 45.4 | 4.6 | 110 |
| (P.B.S.x482B)(Onas x Pre.) | 49.9 | 46.8 | 3.1 | 107 |
| (Dick.x482B)(Onas x482B) | 48.7 | 43.0 | 5.7 | 113 |
| (P.B.S.x482B)(Onas x482B) | 48.7 | 44.4 | 4.3 | 110 |
| (P.B.S.xDick.)(Master x Pre.) | 48.4 | 52.5 | -4.1 | 92 |
| (Dick.xOnas)(P.B.S.x482B) | 45.7 | 49.0 | -3.3 | 93 |
| Mean | 51.9 | 47.4 | 4.6 | 110 |

Mean yields of single, triple and double crosses in the $F_3$ generation exceed the parental average by 5, 3 and 10 per cent respectively, as compared with 19, 24 and 34 per cent for the $F_2$ generation in 1942 (32). The double crosses have consistently displayed the greatest amount of hybrid vigor and appear to be more capable of retaining it. Only two of the double crosses yielded less than the parental average.

The results obtained for tests reported in Part I of this thesis also afford comparisons of the bulk hybrid yield and the parental average. Immer (18) has shown that in barley crosses the $F_1$ exceeded the average of the parents in yield per plant by 27.3 per cent. The results in Table XXI, for Test 3, show that the $F_1$ hybrid average exceeds the parental average by 13 per cent for yield per plant. Great variations in hybrid vigor, ranging from 51 per cent to minus 12 per cent, are apparent. The same crosses in the $F_2$ generation have shown an equal amount of hybrid vigor for yield (as measured in bushels per acre) (Table XXII). Only one cross, namely Thatcher x Reward, yielded less than the parental average. It is suspected that some incompatability may exist between Thatcher and Reward as evidenced by a trace of sterility exhibited in the $F_2$ population.

Immer (18) with barley and Taylor (32) with wheat found that a close relationship exists between hybrid yields and the parental averages. In the present study the $F_2$ hybrid yields for twenty-one crosses were correlated with the parental averages and a non-significant coefficient of 0.232 was obtained. The correlation surface in Figure 11 clearly shows the lack of relationship.

TABLE XXI

Comparison of $F_1$ Hybrid Yields With the Parental Average.

| | Yield (gms./plant) | | | |
|---|---|---|---|---|
| | $F_1$ | Par. Av. | $F_1$ Min. Par. Av. | $F_1$ in % of Par. Av. |
| Erythro x Lutescens | 20.8 | 13.8 | 7.0 | 151 |
| Canus x Lutescens | 17.3 | 13.6 | 3.7 | 127 |
| Lutescens x Red Bobs | 15.8 | 13.2 | 2.6 | 120 |
| Erythro x Comet | 15.3 | 12.2 | 3.1 | 125 |
| Canus x Erythro | 15.2 | 13.0 | 2.2 | 117 |
| Lutescens x Comet | 15.1 | 12.8 | 2.3 | 118 |
| Erythro x Red Bobs | 14.8 | 12.6 | 2.2 | 117 |
| Thatcher x Lutescens | 14.7 | 12.2 | 2.5 | 120 |
| Erythro x Thatcher | 13.6 | 11.6 | 2.0 | 117 |
| Erythro x Reward | 13.3 | 10.0 | 3.3 | 133 |
| Canus x Comet | 12.6 | 12.0 | 0.6 | 105 |
| Lutescens x Reward | 12.2 | 10.6 | 1.6 | 115 |
| Comet x Red Bobs | 12.1 | 11.6 | 0.5 | 104 |
| Canus x Red Bobs | 11.6 | 12.4 | -0.8 | 94 |
| Canus x Reward | 11.0 | 9.8 | 1.2 | 112 |
| Red Bobs x Reward | 10.9 | 9.4 | 1.5 | 116 |
| Canus x Thatcher | 10.6 | 11.4 | -0.8 | 93 |
| Thatcher x Red Bobs | 10.4 | 11.0 | -0.6 | 94 |
| Thatcher x Comet | 9.9 | 10.6 | -0.7 | 93 |
| Comet x Reward | 9.6 | 9.0 | 0.6 | 107 |
| Thatcher x Reward | 7.4 | 8.4 | -1.0 | 88 |
| Mean | 13.0 | 11.5 | 1.6 | 113 |
| Min. Sig. Diff. | 2.9 | - | - | - |

TABLE XXII

Comparison of $F_2$ Hybrid Yields with the Parental Average.

| | Yield (bu./ac.) | | | $F_2$ in % of |
|---|---|---|---|---|
| | $F_2$ | Par. Av. | $F_2$ Min. Par. Av. | Par. Av. |
| Erythro x Comet | 74.8 | 53.8 | 21.0 | 139 |
| Thatcher x Comet | 72.8 | 60.9 | 11.9 | 120 |
| Erythro x Thatcher | 68.3 | 59.1 | 9.2 | 116 |
| Erythro x Lutescens | 67.7 | 52.0 | 15.7 | 130 |
| Lutescens x Red Bobs | 66.4 | 55.2 | 11.2 | 120 |
| Canus x Thatcher | 66.2 | 58.2 | 8.0 | 114 |
| Canus x Lutescens | 64.6 | 51.2 | 13.4 | 126 |
| Canus x Comet | 63.8 | 53.0 | 10.8 | 120 |
| Thatcher x Red Bobs | 63.1 | 62.3 | 0.8 | 101 |
| Comet x Reward | 63.0 | 54.0 | 9.0 | 117 |
| Canus x Reward | 62.4 | 51.3 | 11.1 | 122 |
| Thatcher x Lutescens | 62.2 | 59.1 | 3.1 | 105 |
| Erythro x Reward | 61.8 | 52.2 | 9.6 | 118 |
| Erythro x Red Bobs | 60.7 | 55.2 | 5.5 | 110 |
| Lutescens x Comet | 59.8 | 53.8 | 6.0 | 111 |
| Comet x Red Bobs | 58.8 | 57.0 | 1.8 | 103 |
| Red Bobs x Reward | 58.2 | 55.4 | 2.8 | 105 |
| Thatcher x Reward | 57.7 | 59.2 | -1.5 | 97 |
| Canus x Erythro | 56.7 | 51.2 | 5.5 | 111 |
| Canus x Red Bobs | 56.2 | 54.4 | 1.8 | 103 |
| Lutescens x Reward | 53.6 | 52.2 | 1.4 | 103 |
| Mean | 62.8 | 55.3 | 7.5 | 114 |
| Min. Sig. Diff. | 6.7 | - | - | - |

A highly significant correlation coefficient of 0.554 was obtained between the $F_3$ hard wheat hybrid yields and the parental averages. A non-significant correlation coefficient of 0.026 was obtained between the $F_3$ soft wheat hybrid yields and the parental averages. The correlation surfaces are shown in Figure 12. It is interesting to note that in 1942 the relationship between the $F_2$ hybrid yields and their parental averages was also much better for the hard than for the soft wheat hybrids. Perhaps the poor relationship for the soft wheats is due to large differences in the parental varieties. Two distinct classes of wheat have been crossed to give many of the combinations.

It is reasonable to suppose that, owing to differential segregation, the $F_3$ hybrid yields would be less closely related to the parental averages than would those of the $F_2$. If it is possible to base conclusions on the comparison of the 1942 and 1943 yields, the supposition is supported. A far less consistent display of hybrid vigor was demonstrated in the $F_3$ in 1943 for both the hard and soft wheat hybrids.

As mentioned previously, Taylor (32) had only a limited number of single crosses in both the $F_2$ and $F_3$ generations. It is fairly well established that as homozygosity is reached, hybrid vigor is lost. Harrington (13) and Taylor (32) with wheat hybrids have shown a decrease in the $F_3$ yields as compared to the $F_2$. In the present study, six hard wheat hybrids in the $F_2$ and $F_3$ generations were common to both the 1942 and 1943 tests. A comparison of the results obtained is shown in Table XXIII. Within each

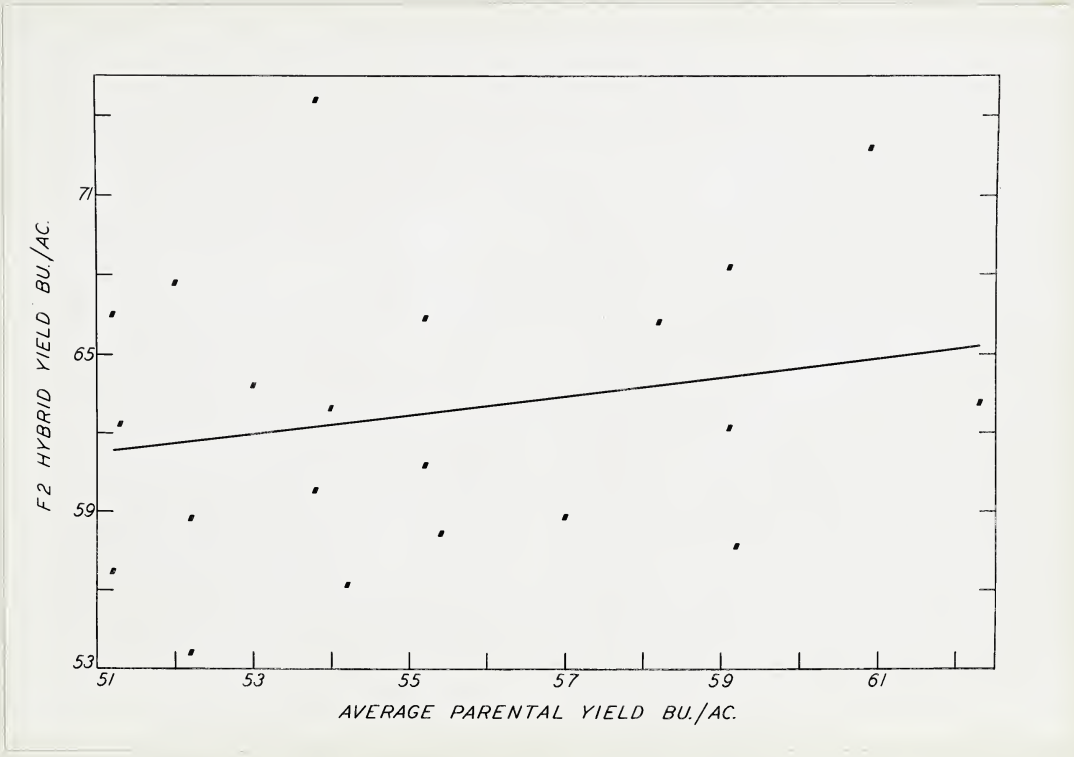



Figure 11.

Relation between $F_2$ yields and parental averages in the Special $F_2$ Wheat Test.

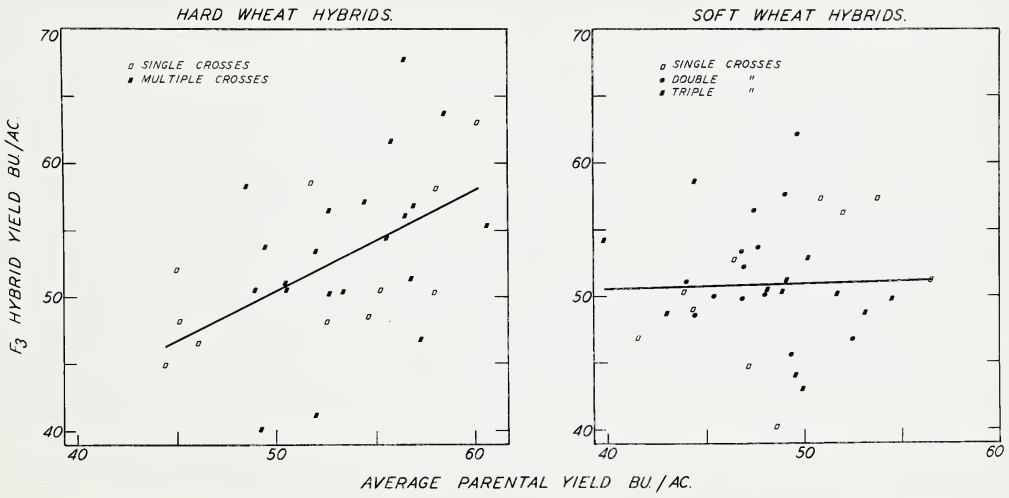



Figure 12.

Relation between $F_3$ yields and parental averages in the Special Hybrid Hard Wheat Test and the Special Hybrid Soft Wheat Test.

TABLE XXIII

Two-Year Comparisons of the Yields of $F_2$ and $F_3$ Generation Hard Wheat Bulk Hybrids.

| | Yield (bu./ac.) | | | | | |
|---|---|---|---|---|---|---|
| | $F_2$ | $F_3$ | Par. Av. | $F_2$ Min. $F_3$ | $F_2$ Min. Par.Av. | $F_3$ Min. Par.Av. |
| **1942 Results** | | | | | | |
| H-37-30 x 482B | 68.2 | 47.7 | 56.8 | 20.5 | 11.4 | -9.1 |
| H-29-35 x Reward | 61.1 | 45.6 | 49.8 | 15.5 | 11.3 | -4.2 |
| Canus x Thatcher | 65.4 | 50.7 | 57.3 | 14.7 | 8.1 | -6.6 |
| Red Bobs x Reward | 59.5 | 49.6 | 53.4 | 9.9 | 6.1 | -3.8 |
| H-37-30 x Canus | 74.1 | 66.7 | 65.7 | 7.4 | 8.4 | 1.0 |
| Canus x Red Bobs | 65.0 | 58.7 | 63.6 | 6.3 | 1.4 | -4.9 |
| Mean | 65.6 | 53.2 | 57.8 | 12.4 | 7.8 | -4.6 |
| % of Par. Av. | 113. | 92. | | | | |
| **1943 Results** | | | | | | |
| Canus x Thatcher | 60.4 | 50.5 | 55.6 | 9.9 | 4.8 | -5.1 |
| Canus x Red Bobs | 67.5 | 63.0 | 60.1 | 4.5 | 7.4 | 2.9 |
| Red Bobs x Reward | 62.4 | 58.1 | 58.0 | 4.3 | 4.4 | 0.1 |
| H-37-30 x 482B | 49.4 | 48.3 | 45.2 | 1.1 | 4.2 | 3.1 |
| H-37-30 x Canus | 48.5 | 48.5 | 54.7 | 0.0 | -6.2 | -6.2 |
| H-29-35 x Reward | 46.1 | 58.6 | 51.7 | -12.5 | -5.6 | 6.9 |
| Mean | 55.7 | 54.5 | 54.2 | 1.2 | 1.5 | 0.3 |
| % of Par. Av. | 103. | 100. | | | | |
| **Average (1942 & 1943)** | | | | | | |
| Canus x Thatcher | 62.9 | 50.6 | 56.4 | 12.3 | 6.5 | -5.8 |
| H-37-30 x 482B | 58.8 | 48.0 | 51.0 | 10.8 | 7.8 | -3.0 |
| Red Bobs x Reward | 61.0 | 53.8 | 55.6 | 7.2 | 5.4 | -1.8 |
| Canus x Red Bobs | 66.2 | 60.8 | 61.8 | 5.4 | 4.4 | -1.0 |
| H-37-30 x Canus | 61.2 | 57.6 | 60.2 | 3.6 | 1.0 | -2.6 |
| H-29-35 x Reward | 54.9 | 52.1 | 50.7 | 2.8 | 4.2 | 1.4 |
| Mean | 60.8 | 53.8 | 56.0 | 7.0 | 4.9 | -2.1 |
| % of Par. Av. | 109. | 96. | | | | |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | |
| | | | | | | | | | | | |
| | | | | | | | | | | | |

group the crosses are arranged in descending order of the difference between the $F_2$ and $F_3$. With the exception of H-29-35 x Reward for 1943, the $F_3$ yields are equal to or lower than the $F_2$. The difference is particularly marked in the 1942 results. On the average, however, the decreases in yield range from 2.8 to 12.3 bushels per acre, representing a loss in hybrid vigor for yield of 7 bushels per acre or 13 per cent. Expressed in per cent of the parental average the $F_2$ and $F_3$ yields are 109 per cent and 96 per cent respectively. In general, the crosses with the greatest amount of hybrid vigor for yield in the $F_2$ are the ones with the greatest reduction in yield in the $F_3$. The average results are obviously predominated by the 1942 results in this respect. The need for more than one year's testing is well illustrated by the results in Table XXIII.

In the Special hybrid soft wheat test, eight crosses were present in both the $F_2$ and $F_3$ generations. Only two of the $F_3$ hybrids yielded more than their respective $F_2$ populations (Table XXIV). On the average the $F_2$ exceeded the $F_3$ by 2.9 bushels per acre. This represents a loss of approximately 6 per cent in hybrid vigor for yield by the $F_3$. The $F_2$ and $F_3$ hybrid yields were found to be fairly closely related to the parental average. Non-significant correlation coefficients of 0.500 and 0.616 respectively were obtained. (See figure 13). The lack of significance is probably due to the limited number of comparisons available. The closeness of the relation between the $F_2$ and $F_3$ hybrid yields and the parental average, and the relative positions of the $F_2$ and $F_3$ hybrid yields and the parental average

are shown graphically in Figure 14. The results for Pacific Bluestem and 482B appear to exhibit a striking exception to the general trend, which suggests that crosses from parents having a low yield themselves tend to yield poorly.

TABLE XXIV

Comparison of the Yields of $F_2$ and $F_3$ Generation Soft Wheat Bulk Hybrids, 1943.

| | Yield (bu./ac.) | | | | $F_2$ in % of Par. Av. | $F_3$ in % of Par. Av. | $F_3$ in % of $F_2$ |
|---|---|---|---|---|---|---|---|
| | $F_2$ | $F_3$ | $F_2$ Min. $F_3$ | Par. Av. | | | |
| P.B.S. x Dicklow | 53.2 | 51.1 | 2.1 | 56.4 | 94 | 91 | 96 |
| P.B.S. x Onas | 60.3 | 57.4 | 2.9 | 53.7 | 112 | 107 | 95 |
| P.B.S. x Pre. | 59.4 | 56.3 | 3.1 | 52.0 | 114 | 108 | 95 |
| Dicklow x Onas | 65.8 | 57.4 | 8.4 | 50.8 | 130 | 113 | 87 |
| P.B.S. x 482B | 44.1 | 44.7 | -0.6 | 47.2 | 93 | 95 | 101 |
| Onas x Prelude | 53.6 | 52.7 | 0.9 | 46.4 | 116 | 114 | 98 |
| Dicklow x 482B | 56.8 | 49.0 | 7.8 | 44.3 | 128 | 111 | 86 |
| Onas x 482B | 45.7 | 46.9 | -1.2 | 41.6 | 110 | 113 | 103 |
| Mean | 54.9 | 51.9 | 2.9 | 49.0 | 112 | 106 | 95 |

Immer (18), working with barley hybrids, has shown that a progressive reduction in yield took place for the $F_2$, $F_3$ and $F_4$ generations. In the present study, eight crosses occurring in the test of hard wheat hybrids were present in the $F_2$, $F_3$ and $F_4$ generations. The results in Table XXV, despite minor inconsistencies, show hybrid vigor for yield in all three generations. The $F_2$ and $F_3$, on the average, have yielded the same, but the $F_4$ has given a greater yield. Expressed in per cent of the parental average, the figures for the $F_2$, $F_3$, and $F_4$ generations are 103, 103 and 110 per cent respectively. With a comparison of ten crosses the $F_2$

was found to exceed the $F_3$ by three per cent. The $F_2$ hybrid yield was found to be closely related to the parental average as indicated by a highly significant correlation coefficient of 0.822. The $F_3$ hybrid yield was less closely related to the parental average as indicated by a coefficient of 0.691, which is significant beyond the five per cent point. A poorer relationship existed between the $F_4$ hybrid yield and the parental average. A non-significant coefficient of 0.656 was obtained. The foregoing relationships are shown in Figure 13. Figure 15 illustrates graphically the tendency for the low-yielding parents to produce low yielding offspring. A progressive reduction in yield for successive generations in barley hybrids (18) is not supported by the present results. It would appear that the high yielding segregates have begun to predominate in the populations of the $F_4$ generation. The fact that the $F_3$ and $F_4$ generation hybrids are progressively less closely related to the parental average than the $F_2$ seems to indicate that differential segregation is taking place.

TABLE XXV

Comparison of the Yields of $F_2$, $F_3$ and $F_4$ Generation Hard Wheat Bulk Hybrids, 1943.

| | Yield (bu./ac.) | | | | $F_2$ in % of | $F_3$ in % of | $F_4$ in % of |
|---|---|---|---|---|---|---|---|
| | $F_2$ | $F_3$ | $F_4$ | Par. Av. | Par.Av. | Par.Av. | Par.Av. |
| Canus x Red Bobs | 67.5 | 63.0 | 65.7 | 60.1 | 112 | 105 | 109 |
| Red Bobs x 1515-29.27 | - | 50.3 | 58.2 | 58.2 | - | 86 | 100 |
| Red Bobs x Reward | 62.4 | 58.1 | 57.8 | 58.0 | 108 | 100 | 100 |
| Canus x Thatcher | 60.4 | 50.5 | 51.4 | 55.6 | 109 | 91 | 92 |
| H-37-30 x Canus | 48.5 | 48.5 | 64.5 | 54.7 | 89 | 89 | 118 |
| H-37-30 x Reward | 51.0 | 48.2 | - | 52.6 | 97 | 92 | - |
| H-29-35 x Reward | 46.1 | 58.6 | 65.0 | 51.7 | 89 | 113 | 126 |
| 482B x Thatcher | 59.8 | 46.6 | - | 46.1 | 130 | 101 | - |
| H-37-30 x 482B | 49.4 | 48.3 | 54.7 | 45.2 | 109 | 107 | 121 |
| 482B x Canus | 45.2 | 52.0 | 44.9 | 45.0 | 100 | 116 | 100 |
| H-29-35 x 482B | 47.5 | 45.0 | 50.3 | 44.4 | 107 | 101 | 113 |
| 8-cross mean | 53.4 | 53.0 | 56.8 | 51.8 | 103 | 103 | 110 |
| 10-cross mean | 53.8 | 51.9 | - | 51.3 | 105 | 102 | - |

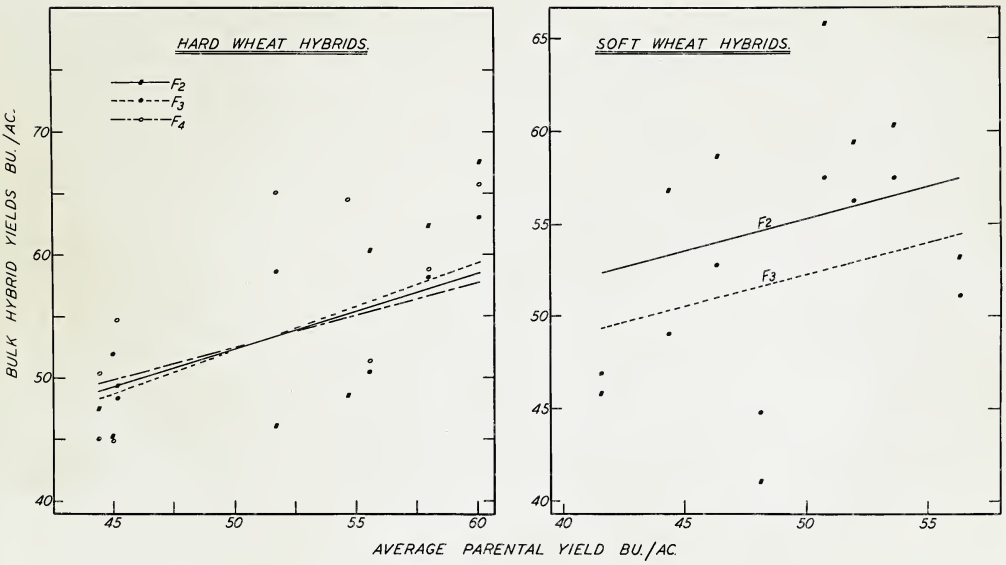



Figure 13.

Relations between $F_2$, $F_3$ and $F_4$ yields and parental averages for Hard Wheat Hybrids and between $F_2$ and $F_3$ yields and parental averages for Soft Wheat Hybrids.

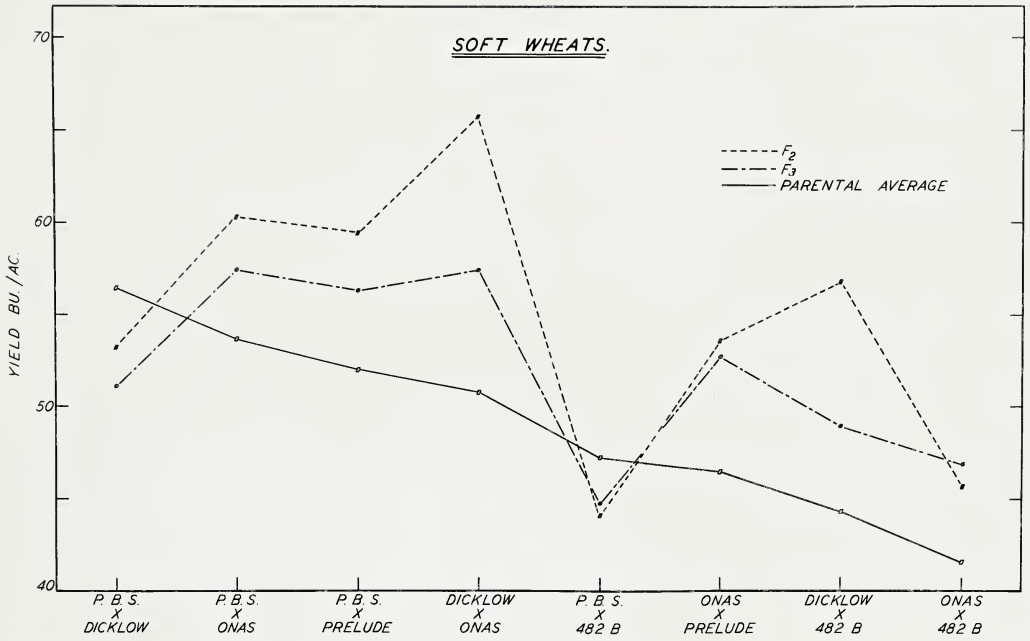



Figure 14.

Graph showing the relation between the $F_2$ and $F_3$ yields and the parental averages for eight soft wheat single crosses.

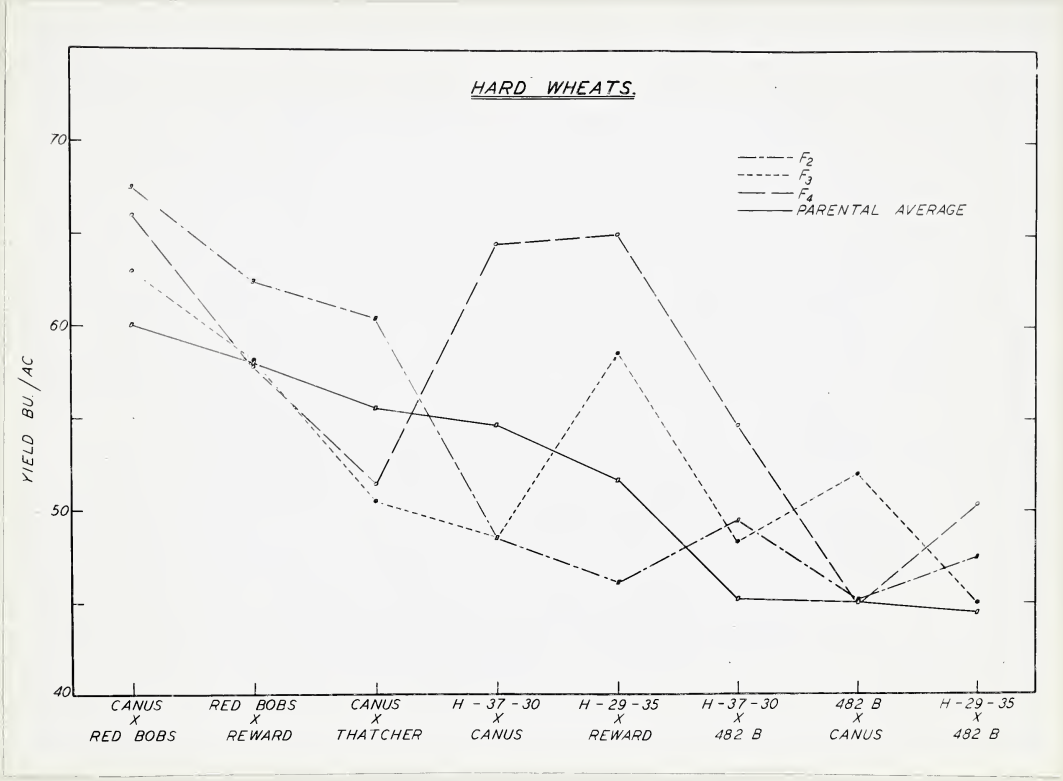



Figure 15.

Graph showing the relation between the $F_2$, $F_3$, and $F_4$ yields and the parental averages for eight hard wheat single crosses.

Earliness.

Taylor (32) and Darroch (6) are among the many workers who have demonstrated a close relationship between yield and maturity. Florell, and Clark and Hooker, cited by Taylor (32), found that earliness was dominant in the $F_2$ and $F_3$ generations. Taylor's results show that all but a few $F_3$ hybrid populations headed and matured earlier than the parental average.

The only results obtained in the present study to indicate earliness were "days to heading". Taylor (32) is among others who have repeatedly demonstrated a close relationship between "days to heading" and "days to maturity". It may, therefore, be concluded that days to heading is a good indication of maturity.

The results in Table XXVI show that all hybrid populations, regardless of generation, are earlier than the parental average. The hard wheat single crosses appear to become progressively earlier as homozygosity is reached. Such a condition is not in agreement with the 1942 results (32).

The writer has repeatedly observed that high yield has been accompanied by late maturity.* It has already been shown (Table XXV) that the single cross $F_4$ hard wheat hybrids yielded more, in bushels per acre, than the same $F_2$ or $F_3$ populations, yet Table XXVI shows these same $F_4$ hybrids to be earlier than the $F_2$ or $F_3$ populations. It is the writer's belief that since 1943 was a year which favored early maturing varieties, early maturing

---

*Drought breeding program, Department of Field Crops.

TABLE XXVI

Comparison of the Growth Period of Single and Multiple Hard and Soft Wheat Hybrids with the Parental Average.

| No. of Hybrids | Crosses | Hybrid Av. | Par. Av. | Hyb. Av. Minus Par. Av. | Hyb. Av. in % of Par. Av. |
|---|---|---|---|---|---|
| | SPECIAL HYBRID HARD WHEAT | | | | |
| 10 | Single Crosses $F_2$ | 73.1 | 74.2 | -1.1 | 98.5 |
| 11 | Single Crosses $F_3$ | 72.5 | 73.8 | -1.3 | 98.2 |
| 9 | Single Crosses $F_4$ | 72.3 | 73.9 | -1.6 | 97.8 |
| 6 | Triple Crosses $F_3$ | 74.5 | 74.7 | -0.2 | 99.7 |
| 2 | Double Crosses $F_2$ | 72.5 | 73.5 | -1.0 | 98.6 |
| 11 | Double Crosses $F_3$ | 72.1 | 73.3 | -1.2 | 98.4 |
| 2 | 5-Variety Crosses $F_3$ | 72.5 | 73.8 | -1.3 | 98.2 |
| 3 | 6-Variety Crosses $F_3$ | 73.3 | 74.3 | -1.0 | 98.6 |
| 1 | 8-Variety Crosses $F_3$ | 73.0 | 73.5 | -0.5 | 99.3 |
| | SPECIAL HYBRID SOFT WHEAT | | | | |
| 8 | Single Crosses $F_2$ | 76.1 | 77.4 | -1.3 | 98.3 |
| 10 | Single Crosses $F_3$ | 74.4 | 75.6 | -1.2 | 98.4 |
| 11 | Triple Crosses $F_3$ | 73.4 | 74.7 | -1.3 | 98.2 |
| 14 | Double Crosses $F_3$ | 74.4 | 75.5 | -1.1 | 98.5 |

segregates have begun to predominate in the populations as homozygosity is reached. The large part which a factor like maturity plays in determining yield emphasizes the need for results of more than one year's testing.

Combining Ability of Parents.

The material used in the studies reported in Part I of this thesis provides ideal comparisons to determine the combining ability of parents. Each of seven varieties was crossed with each other variety to give a complete set of twenty

one crosses. Reciprocal crosses, however, were not made. The results in Figure 16 were obtained from the following sources:

| | | |
|---|---|---|
| Total seed yield (gms. per plant) $F_1$ | .. | Test 3. |
| No. of seeds, main culm, $F_1$ | .. | Test 3. |
| No. of tillers $F_1$ | .. | Test 3. |
| Height in inches $F_1$ | .. | Average of Tests 1, 2, and 3. |
| Days to heading $F_1$ | .. | Average of Tests 1 and 2. |
| Days to heading $F_2$ | .. | Special $F_2$. |
| Yield in bus. per acre $F_2$ | .. | Special $F_2$. |

The figures for crosses were obtained by averaging the six crosses in which one particular variety was a common parent. The parental figures are simply those results obtained for the individual parents. An example may clarify the situation. The Red Bobs figure for crosses is an average of the results obtained for the crosses in which Red Bobs is combined with the other six varieties. The result for Red Bobs alone is indicated in the line for parents.

For each character illustrated in Figure 16 the varieties are arranged in decreasing magnitude of the cross average. This arrangement facilitates the observation of the value of various parents. Late varieties are favored by such an arrangement and this should be taken into consideration in a study of the Figure. Late maturing varieties are not necessarily most desirable.

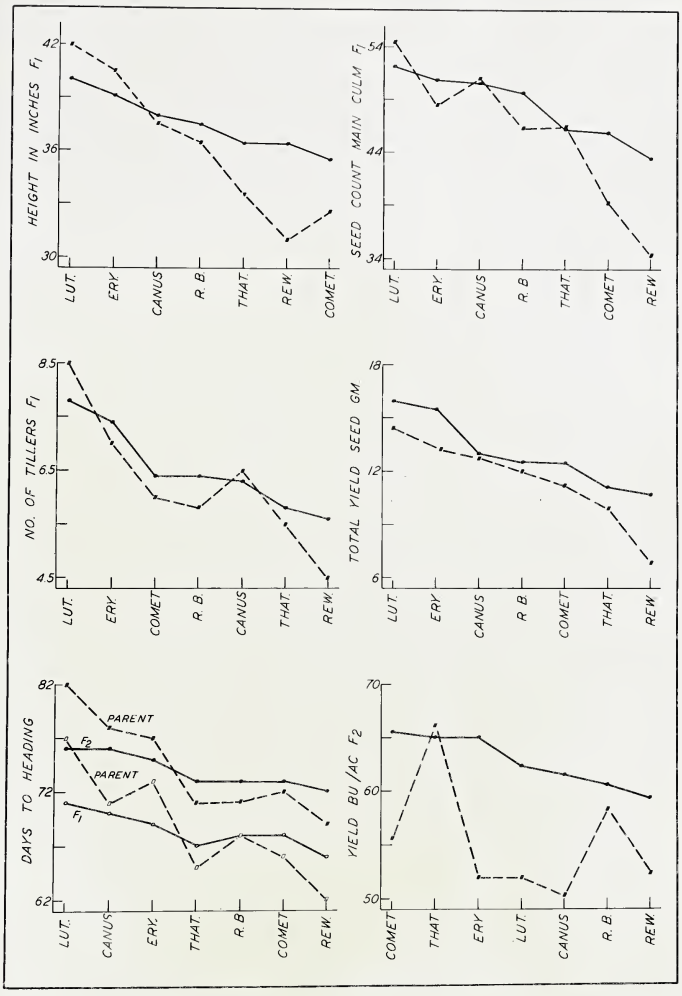



Figure 16.

Graphs showing the parental effects in crosses involving each parent on various agronomic characters. The solid lines represent averages of six crosses. Dotted lines refer to performances of a single parent.

Considerable information is contained in Figure 16. With the exception of "yield in bushels per acre $F_2$", Lutescens consistently places first and Reward always last. As mentioned earlier, the yield of late maturing varieties in the Special $F_2$ test was seriously affected by incomplete filling. This is clearly evident in Figure 16. In support of the findings of Taylor (32) the results for parental varieties appear to be a valuable indication of their combining ability. There is no indication of exceptional parents, i.e. those parents capable of producing an unusually high percentage of superior selections in their offspring (11). There is considerable evidence of hybrid vigor and although the hybrid average is exceeded by the parent for some varieties, it should be remembered that the figure for the hybrid is an average of six, while that of the parent is an individual result.

Quite aside from the combining ability of parents, the interrelationship of characters is illustrated in Figure 16. The association of height, number of tillers, yield and maturity is not only outstanding, but consistent throughout. Lutescens is tall, late, high yielding and tillers well. Reward is short, early, low yielding and produces only a few tillers. Yield alone cannot safely be used as the criterion to judge the value of a parent. A valuable parent is one which combines a maximum number of desirable with a minimum of undesirable characters. The interrelationship is not only complex, but variable. One character may be decidedly important one year and relatively insignificant another.

## DISCUSSION.

The use of bulk hybrid yield tests as a basis for discarding certain crosses has been advocated by several workers (11, 13, 18) on the assumption that the proportion of high yielding genotypes in the low-yielding crosses will be less than in crosses with a higher average yield. The results of the present investigation and of the study by Taylor (32) have demonstrated that hybrid populations differ greatly in yield. If one is to consider that yield alone is the most desirable character, then it seems possible to conclude that at least a rough evaluation of hybrid populations could be made on the basis of yield. Perhaps a greater number of genotypes could be taken from the high yielding crosses.

It seems imperative that any evaluation of yield must be based on not less than two years' testing. Environment plays a large part in determining the complex called "yield". Hybrid populations or varieties favored by a set of conditions one year may be equally retarded by another set of conditions the next year. Among a multiplicity of characters, yield is affected by maturity and straw strength, as was illustrated by the results of the hard wheat hybrid yield test in 1943. Little relationship between these results and the results for 1942 indicates that the results for either year must be treated with caution. The fact that the results of a whole year's testing may be rendered invalid by environmental conditions suggests that conclusions should be based on several tests. Accepting this, bulk hybrid yield tests immediately fall into the category of rod-row tests and are therefore subject

to the same limitations such as labor and cost of handling. Furthermore, the amount of seed available is a factor usually limiting the extensiveness of bulk hybrid tests. It has been suggested (32) that, in addition to the possibility of obtaining sufficient seed for a fully replicated yield test, if the bulk hybrids were allowed to segregate in the $F_2$ and yield tests conducted in the $F_3$ and $F_4$ generations, a more accurate evaluation of the hybrids as a source of high yielding segregates might be obtained. Yield tests of the $F_3$ and $F_4$ would be less complicated by hybrid vigor and the yields obtained would represent to a greater degree the actual yields of the segregates themselves. There remain, nevertheless, the problems of mixing when handling and loss of vitality during storage. To provide comparable material not only should there be sufficient seed for one year's test, but also enough for two or three tests.

The following extract from a paper by Worzella (37) clearly demonstrates that yield alone cannot be taken as a criterion of the value of a variety:

> "Because of the varied demands for wheats and their products, the objectives cannot be static but must be ever changing. Our aim is, not only a stable wheat crop, but also one that is more uniform and superior in quality to our present wheats. We do not want varieties that produce large crops some years and failures in others, but rather those that are able to resist the rigors of hard winters, drought, delayed harvests, etc., and that produce a uniform crop. Since wheat is the raw material that goes into the production of many foods and other products, new varieties must be "built up" to meet the requirements of these specific demands."

Bulk hybrid yield tests obviously have little place in the development of these varieties.

Studies on hybrid vigor are not new. Many workers (7, 8, 28, 30, 32) have reported the presence of hybrid vigor in cereals, and such a factor must obviously be considered in the present study. Varying amounts of vigor or lack of vigor have been found. In general the results of the present study agree fairly well with the findings of others in that hybrid vigor is lost as homozygosity is reached. There appears to be a tendency for those crosses with the greatest amount of hybrid vigor in the $F_2$ to have the greatest reduction in yield in the $F_3$. Such a condition emphasizes that results of bulk hybrid yield tests should be interpreted with caution.

It has previously been mentioned that certain workers (10, 23, 31) have found that the yields of varieties in mixed stands are not necessarily correlated with those of the same varieties grown separately. If such findings are accepted, the limitation of bulk progeny yield tests to determine the value of a particular cross is immediately apparent. Advocates of this method commonly assume that the forces of natural selection which favor the perpetuation of plants that are best fitted to survive in the hybrid mixtures will likewise sort out the types that will yield best when grown alone. High yielding populations may not, therefore, be the ones which will eventually produce a high percentage of superior segregates. If, however, the undesired types are being eliminated by such adverse factors as cold, disease or susceptibility to insect attack, then the plants which survive in the hybrid mixtures will, in all probability, be the ones which are most capable of giving good yields when grown alone.

Artificial selection cannot be practiced on hybrid populations in yield tests, otherwise the plant breeder defeats

the purpose for which they were intended. The writer is firmly convinced that modern plant breeding methods should select for resistance to disease and insects as well as drought and cold. Quality, strength of straw, and other desirable agronomic characters should also be sought in segregating populations. The mass - pedigree method advocated by Harrington (12) may be utilized advantageously. Waldron (34) has suggested a positive relation between frost resistance and drought resistance. This relation is now being utilized in some breeding programs and appears to hold considerable promise for the selection of superior varieties.

An important aim of the present study has been to determine, if possible, the relative value of multiple cross hybrids. There is evidence that six and eight-variety crosses in the hard wheats and double crosses in the soft wheats have retained their hybrid vigor better than single crosses. It may be that there has been a high concentration of desirable characters in these multiple crosses to form a more stable unit. It is thought that, within reasonable limits, multiple crosses may be a good source of valuable segregates.

Taylor (32) has emphasized the importance of having crosses complete to facilitate the study of the combining ability of parents. In the present study, twenty-one crosses were available, involving seven varieties in all possible combinations. Varieties differed in their combining ability as measured by the characters: yield, number of tillers, height and days to heading. The importance of balancing the various attributes of a variety in determining its combining ability is clearly demonstrated.

## SUMMARY

This continuation of a study to determine the behaviour of single and multiple hybrid populations in early generations, as a basis for discarding low yielding crosses, has utilized a large number of hard and soft wheat bulk populations in replicated yield tests.

Yield levels for 1942 and 1943 were similar but in other comparisons there was considerable disparity. Results for the two years' tests of soft wheat hybrids were more closely related than those for the hard wheat hybrids.

Hybrid vigor for yield was not so consistent in 1943 as in 1942. The average for all hybrid populations showed hybrid vigor for maturity. Six and eight-variety hard wheat hybrids and double cross soft wheat hybrids appeared most capable of retaining their hybrid vigor for yield, indicating the possibility that these crosses might be a good source of high yielding segregates.

For a limited number of hard and soft wheat single crosses, the $F_3$ on the average yielded less than the $F_2$. The few $F_4$ hard wheat single crosses available gave yields greater than either the $F_2$ or $F_3$ generations.

Only very slight relations existed between the hybrid populations and their parental averages. While some fairly close relationships were found for a few groups of crosses, it can hardly be concluded that the parental average is a good indication of the value of a cross.

The yield of a variety appears to be a good indication of its combining ability. Such other factors as height, number of

tillers and maturity should not be overlooked in the determination of the value of a variety.

Even if the disparity in the results obtained for two years' testing of a large number of single and multiple hybrid populations is ignored, it is thought that the use of yield tests of unselected bulk populations in early generations as a basis for discarding those crosses which will eventually give only a few high-yielding segregates, has no place in a modern plant breeding program.

## GENERAL DISCUSSION.

Improved or short-cut methods of selecting promising material from hybrid populations are constantly being sought by the plant breeder. It is a relatively simple matter to make crosses in wheat and produce thousands of new genotypes, but it is very difficult to recognize the most valuable segregates in this large mass of material. A cross is made between two varieties in the hope of getting something superior in yield, drought resistance, etc., and this is possible only when the characters can be recognized and measured accurately.

The relationship between stomatal size (length) and yield has been studied for seven parental varieties and twenty-one $F_1$ hybrid populations. If the assumptions of Birdsall (2) and Darroch (6) are correct, it should be possible to eliminate poor yielding lines from hybrid populations on the basis of stomatal size. Undoubtedly this assumption would be true if there were any "best" stomatal size. It is true that varieties differ in their stomatal size, but the relation between stomatal size and yield is not constant.

Selection for yield on the basis of protein content should be a valuable aid to the plant breeder. Notwithstanding minor discrepancies, Neatby and McCalla (22) concluded from a study of the relation between protein and yield that the differences are remarkably constant from station to station. They suggest that selection for protein content can be undertaken at any one station with confidence.

In contrast to stomatal size, there appears to be an optimum protein content above or below which hybrid lines may be discarded. The high protein lines yield poorly, while the low protein lines, regardless of yield, are inferior in quality. The measuring of protein content is a relatively simple procedure, but cannot be done until sufficient seed is available. If there were a satisfactory relationship between stomatal size and yield, selection could be made on the basis of single plants. For a reliable test, however, the plants should be homozygous so that even if there were a satisfactory relationship only one year would be saved.

It is possible that a few hybrid lines would behave in an irregular manner with regard to protein content. These would be apparent on a correlation surface and could be dealt with individually. Where a relationship between stomatal size and yield cannot be used, protein content should serve a useful purpose. The plant breeder should have little hesitation, after subjecting hybrid populations to diseases, insects, cold, etc., to further reduce the surviving lines on the basis of protein content, Stomatal size has no such value.

Replicated yield tests of a large number of unselected bulk populations of hard and soft wheat hybrids were conducted in the field to permit a study of the behaviour of single and multiple crosses in early generations. It was hoped that the results obtained would give information regarding the potential value of these crosses as sources of high-yielding segregates.

Hybrid populations differed in their ability to yield, and it is considered by several workers (11, 13, 18) that these

differences may be used to indicate the potential yielding possibilities of a cross. As is suggested by Taylor (32), for prediction purposes a rough classification might be set up in which the unselected bulk populations could be placed in three groups, namely, promising, average and unpromising.

There are, however, many limitations to the use of yield alone in evaluating hybrid populations. The complexities of yield are recognized (3, 4, 23, 36, 37). There exists, in addition, the fact that natural selection among varieties sown in mixed stands does not always favor the varieties that give the higher grain yields when sown alone under the same conditions (10, 23, 31).

An extensive study by the writer* of varietal changes in wheat, oats, barley and flax has revealed that in recent years new varieties nearly always possess disease or other resistance. Yield tests of bulk populations eliminate the possibility of practising artificial selection and, therefore, greatly retard the recognition of superior segregates. The aim of the modern plant breeder is to produce a variety which is able to resist the rigors of weather, diseases, insects, etc. Yield tests of bulk populations cannot be considered a satisfactory method of selecting those crosses which will eventually give a high percentage of superior segregates.

---

*Jenkins, B. C. Some varietal changes in wheat, oats, barley and flax, and some factors contributing to these changes. University of Alberta, Field Crops Course 101, 1942-43.

ACKNOWLEDGEMENTS.

The original plans for the studies outlined in this thesis were drawn up under the direction of Dr. J. W. Boyes, formerly Assistant Professor of Genetics and Plant Breeding, Department of Field Crops, University of Alberta. The bulk of the experimental work and the preparation of this thesis have been carried out under the direction of Dr. A. G. McCalla, Professor of Field Crops, University of Alberta, whose helpful suggestions and criticisms are gratefully acknowledged.

In an investigation of this kind, a considerable amount of assistance is given by junior members of the department staff. To all who have helped in any way, the author wishes to express his sincere thanks.

It is a pleasure to acknowledge financial assistance from the National Research Council of Canada and the Alberta Wheat Pool.

REFERENCES

1. AAMODT, O. S. and JOHNSTON, W. H. Studies on drought resistance in spring wheat. Can. Jour. Res. C14:122-152, 1936.

2. BIRDSALL, J. E. The size and frequency of stomata in relation to drought resistance in wheat. Master's Thesis, University of Alberta, 1940.

3. BONNETT, O. T. and WOODWORTH, C. M. A yield analysis of three varieties of barley. Jour. Amer. Soc. Agron. 23:311-327, 1931.

4. BRIDGFORD, R. O. and HAYES, H. K. Correlation of factors affecting yield in hard red spring wheat. Jour. Amer. Soc. Agron. 23:106-117, 1931.

5. CLARK, J. A. Registration of improved wheat varieties. Jour. Amer. Soc. Agron. 28:66-68, 1936.

6. DARROCH, J. G. The interrelationships of grain yield, stomatal length and soil drought in wheat varieties. Master's Thesis, University of Alberta, 1943.

7. EAST, E. M. Heterosis. Genetics 21:375-397, 1936.

8. ENGLEDOW, F. L. and PAL, B. P. Investigations on yield in cereals. VIII. Hybrid vigor in wheat. Jour. Agr. Sci. 24:390-409, 1934.

9. HABER, E. S. A study of drought resistance in inbred strains of sweet corn. Zea Mays var. Rugosa. Iowa Agr. Expt. Sta. Res. Bull. 243, 1938.

10. HARLAN, H. V. and MARTINI, M. L. The effect of natural selection in a mixture of barley varieties. Jour. Agr. Res. 57:189-199, 1938.

11. HARLAN, H. V., MARTINI, M. L. and STEVENS, H. A study of methods in barley breeding. U. S. D. A. Tech. Bull. 720, 1940.

12. HARRINGTON, J. B. The mass-pedigree method in the hybridization improvement of cereals. Jour. Amer. Soc. Agron. 29:379-384, 1937.

13. HARRINGTON, J. B. Yielding capacity of wheat crosses as indicated by bulk hybrid tests. Can. Jour. Res. C18:578-584, 1940.

14. HARRINGTON, J. B. The effect of having rows different distances apart in rod row plot tests of wheat, oats and barley. Sci. Agr. 21:589-606, 1941.

15. HAYES, H. K. Natural crossing in wheat. Jour. Amer. Soc. Agron. 10:120-122, 1918.

16. HAYES, H. K. and IMMER, F. R. Methods of plant breeding. McGraw-Hill Book Co., New York, 1942.

17. HOPKINS, J. W. Comparative development of two wheat varieties under varying moisture supply. Can. Jour. Res. C17:87-96, 1939.

18. IMMER, F. R. Relation between yielding ability and homozygosis in barley crosses. Jour Amer. Soc. Agron. 33:200-206, 1941.

19. IMMER, F. R. Distribution of yields of single plants of varieties and $F_2$ crosses of barley. Jour Amer. Soc. Agron. 34:844-850, 1942.

20. LEIGHTY, C. E. and TAYLOR, J. W. Studies in natural hybridization of wheat. Jour. Agr. Res. 35:865-887, 1927.

21. MAXIMOV, N. A. The plant in relation to water. (Authorized English translation by R. H. Yapp). Allen and Unwin, London, 1929.

22. NEATBY K. W. and McCALLA, A. G. Correlation between yield and protein content of wheat and barley in relation to breeding. Can Jour. Res. C16:1-15, 1938.

23. PAPADAKIS, J. S. The relation of the number of tillers per unit area to the yield of wheat and its bearing on fertilizing and breeding this plant - the space factor. Soil Sci. 50:369-388, 1940.

24. PETO, H. B. The measurement of drought resistance in wheat by field and laboratory methods. Master's Thesis, University of Alberta, 1937.

25. PLATT, A. W. and DARROCH, J. G. The seedling resistance of wheat varieties to artificial drought in relation to grain yield. Sci. Agr. 22:521-527, 1942.

26. ROBERTSON, D. W. and DEMING, G. W. Natural crossing in barley at Fort Collins, Colorado. Jour. Amer. Soc. Agron. 23:402-406, 1931.

27. ROSENQUIST, C. E. An improved method of producing $F_1$ hybrid seeds of wheat and barley. Jour. Amer. Soc. Agron. 19:968-971, 1927.

28. ROSENQUIST, C. E. Hybrid vigor in wheat. Jour. Amer. Soc. Agron. 23:81-105, 1931.

29. STEVENSON, F. J. Natural crossing in barley. Jour. Amer. Soc. Agron. 20:1193-1196, 1925.

30. SUNESON, C. A. and RIDDLE, O. C. Hybrid vigor in barley. Jour. Amer. Soc. Agron. 36:57-61, 1944.

31. SUNESON, C. A. and WIEBE, G. A. Survival of barley and wheat varieties in mixtures. Jour. Amer. Soc. Agron. 34:1052-1056, 1942.

32. TAYLOR, D. K. A study of parental lines and bulk progenies from single and compound crosses in wheat and barley. Master's Thesis, University of Alberta, 1943.

33. TORRIE, J. H. Inheritance studies of several qualitative and quantitative characters in spring wheat crosses between varieties relatively susceptible and resistant to drought. Can. Jour. Res. C14:368-385, 1936.

34. WALDRON, L. R. Frost injury to spring wheat with a consideration of drought resistance. Jour Amer. Soc. Agron. 23:625-637, 1931.

35. WHITESIDE, A. G. O. Effect of soil drought on wheat plants. Sci. Agr. 21:320-334, 1941.

36. WOODWORTH, C. M. Breeding for yield in crop plants. Jour. Amer. Soc. Agron. 23:388-395, 1931.

37. WORZELLA, W. W. Some objectives in breeding for yield and other agronomic characters in wheat. Jour. Amer. Soc. Agron. 33:174-180, 1941.

# APPENDIX "A"

## Aids to the Measurement of Stomata.

## AIDS TO THE MEASUREMENT OF STOMATA

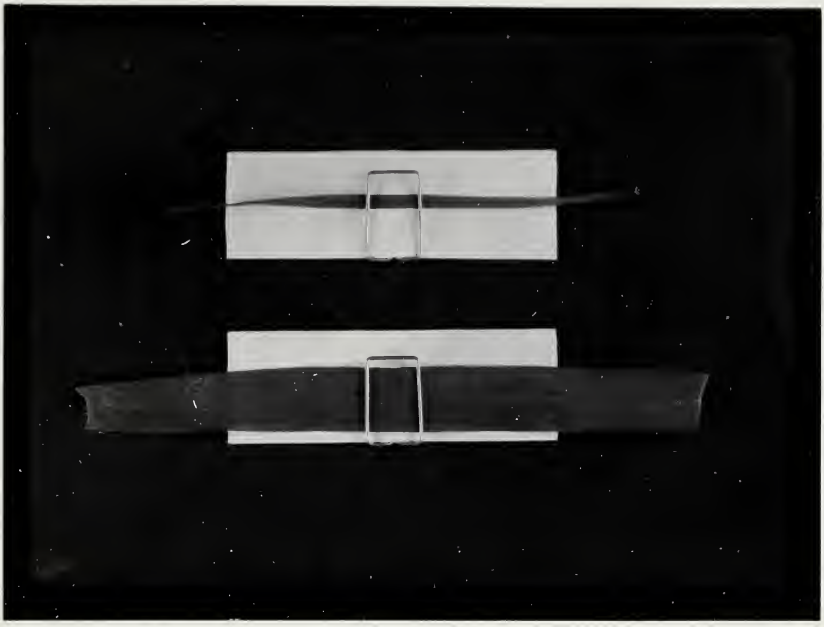
### I. An improved microscope slide.

In studies of stomatal size (length) and frequency, Birdsall (2) made use of 8 x 4 cm. slides on which the leaves were held by means of thin cardboard of the same dimensions, glued to one edge of the slide. In the centre of the cardboard a hole one centimeter in diameter was cut, thus exposing a portion of the leaf. These slides were found to have a number of disadvantages. The slide had to be removed from the microscope stage each time a new leaf was examined. Very often considerable time was lost in an attempt to get the leaf in position. This was especially true of seedling leaves.

A slide which facilitated the more rapid handling of leaves was developed. It consisted of an ordinary microscope slide to which a number 2 Owl paper clip was fastened by cellulose tape. Instead of removing the slide from the stage of the microscope each time a new leaf was required, the leaf was slipped under the clip while the slide remained in position. This allowed a considerable saving of time, with the added advantage that twisted or curled leaves and leaves of any size (see Figure 1) could be handled with relative ease. Very little focal adjustment was necessary since the leaf surface was constantly held flat. An improvement* consisting of the use of waterproof adhesive tape instead of the cellulose tape (which has a tendency to wrinkle when wet) was adopted.

---

*Suggested by Mr. J. G. Darroch.



Appendix "A" - Figure 1.

Improved microscope slide adapted
for leaves of various sizes.

It is the writer's opinion that this slide or a modification of it has a definite place in studies where material of this or a similar nature is examined under the microscope.

II. A rapid method of identifying collected leaves.

The collection and examination of a great many leaves in as short a time as possible necessitated a speedy as well as accurate method of identifying them. Such a method is here described.

Numbers identifying the leaves are written on thin strips of paper. As the leaves are removed, they are placed with the tip beside their respective number and fixed there with a 3/8 inch strip of cellulose tape. (see figure 2.) The numbers are clearly visible through cellulose tape. When a "batch" has been obtained it is rolled up, with the numbers facing outward, starting with the highest number. This makes possible the orderly removal of leaves when stomatal measurements are made.

It is thought that this method of handling leaves has a very useful application in these and similar studies.

Appendix "A" - Figure 2.

"Batch" of numbered leaves ready
for examination under microscope.

## APPENDIX "B".

## Tests of Stage and Position.

## TESTS OF STAGE AND POSITION.

The stage of plant development at the time leaves are taken for stomatal measurements, and the position on the leaf at which readings are made, are important considerations. Birdsall (2) measured the stomata of the first or seedling leaf when plants were in the third leaf stage: of the flag-leaf when the plants had just headed, and of the subterminal leaf when the plants were in the shot blade or just heading. He made his determinations at a position near the base of the leaf, but Darroch (6) took a trans-leaf sample within 1.5 to 2 inches of the leaf tip. Darroch reasoned that the leaf tip is the region where differentiation, maturation, and chlorophyll syntheses are first completed, and would therefore seem to be the most suitable region upon which to base varietal comparisons. That such reasoning is sound is not disputed, but it has been the writer's experience that a higher percentage of abnormally large or abnormally small stomata occur near the leaf tip. The stomata occur in rows parallel to the veins of the leaf, and since there is a tapering off towards the tip, some rows are terminated, while others continue to the tip. Not all the rows can be crowded in the narrow space at the leaf tip.

For the studies reported in Part I of this thesis an intermediate course with regard to position was followed. All measurements of stomata on seedling leaves were made by taking a trans-leaf sample at about the centre of the leaf. All seedling leaves were taken from plants in the 3 to 4-leaf stage and all flag leaves were taken when the head was 2 inches out of the "boot".

Although the position and stages just mentioned were used throughout the entire investigation, a few small tests were conducted to determine, if possible, whether these were satisfactory or not. Three such tests are dealt with briefly in the sections which follow.

I. Experiment to determine proper stage at which seedling leaves should be taken.

Flats of Canus and Thatcher seedlings, two varieties differing markedly in maturity and stomatal size, were grown in the greenhouse in January 1942. Six typical plants were selected from each of these varieties for observations of stomatal size at various stages of growth. Measurements were begun as soon as the seedling leaves were sufficiently well developed, and continued, using the same leaves and the same relative position on the leaves, until they had shrivelled and died. Notes as to the length of the seedling leaf were recorded when the stomata were measured as well as the stage of plant development. A trans-leaf sample of ten stomata per leaf was taken on each date for each leaf. Results of the experiment and the analyses of variance are presented in Tables I and II.

APPENDIX "B" - TABLE I

Length of Seedling Leaf and Stomatal Size as Affected by Time.

| Date | Canus | | Thatcher | |
|---|---|---|---|---|
| | Leaf Length (cm.) | Stomatal Size | Leaf Length (cm.) | Stomatal Size |
| January 9th | 12.4 | 80.8 | 12.7 | 89.5 |
| " 12th | 15.5 | 86.0 | 16.0 | 89.9 |
| " 14th | 15.7 | 84.3 | 16.7 | 88.1 |
| " 16th | 15.8 | 85.2 | 16.8 | 89.8 |
| " 19th | 15.8 | 85.5 | 16.3 | 89.7 |
| " 21st | 15.7 | 85.4 | 16.4 | 89.9 |
| " 23rd | 15.6 | 84.2 | 16.2 | 88.8 |

NOTE: Leaf length figures for each variety represent the average of six measurements. Stomatal size figures for each variety represent the average of sixty measurements.

APPENDIX "B" - TABLE II

Results of the Analyses of Variance of Stomatal Size Measurements for Canus and Thatcher in the "Stage Test".

| Variance due to: | D. F. | Mean Squares | |
|---|---|---|---|
| | | Canus | Thatcher |
| Dates | 6 | 18.52** | 2.86 |
| Plants | 5 | 19.90** | 19.90** |
| Error | 30 | 3.77-- | 3.64-- |
| Total | 41 | | |

**Significant beyond the 1% point.

--

The apparent fluctuation in stomatal size for January 12th and 14th might have been due to error in measuring. It has been noticed that difference in lighting can affect the accuracy of recordings. The lighting in this experiment was not controlled. However, the results presented appear to indicate that once the seedling leaf is fully developed the stomatal size remains relatively constant. This is true regardless of the stage of plant development, since on the first date the second leaf was just appearing while on the last the fourth was visible. The experiment was terminated when the seedling leaf began to turn yellow. It is suggested that within reasonable limits the size of stomata on a seedling leaf is little affected by stage of plant development.

II. Experiment to determine proper stage at which flag leaves should be taken and whether stomatal size varies with different positions on the leaf.

Flag leaves of Red Bobs border material, growing close to Test 3, (see Part I of thesis) were taken from plants at three stages of development. Duplicate leaves were taken from plants at each stage. Stomatal measurements, twenty at each position, were made immediately for three trans-leaf positions on each leaf. The various stages and positions are shown in Table III. After the leaves had been placed in the "cold room" for some time, the measuring was repeated. As might be expected, the stomata were found to be uniformly larger (longer), since the guard cells elongate when the pore is closed.

For the analysis of variance (Table III) and the results (Table IV) the direct and after cold chamber readings were

simply averaged. Figures for each position reported in Table III represent the average of 80 individual stomatal measurements.

APPENDIX "B" - TABLE III

Summary of Stomatal Size Measurements for Three Position on Flag Leaves of Red Bobs Taken at Three Stages of Development.

| | Stage | Position | | | Mean |
|---|---|---|---|---|---|
| | | Base | Centre | Tip | |
| I. | Head just emerging | 60.4 | 59.1 | 57.4 | 59.0 |
| II. | Head 2 inches out | 60.6 | 60.4 | 62.8 | 61.3 |
| III. | Flowering | 61.2 | 60.8 | 62.7 | 61.6 |
| | Mean | 60.7 | 60.0 | 60.9 | |

APPENDIX "B" - TABLE IV

Results of the Analysis of Variance of Stomatal Size Measurements for Three Positions on Flag Leaves of Red Bobs Taken at Three Stages of Development.

| Variance due to: | D. F. | M. S. | F. |
|---|---|---|---|
| Stages | 2 | 120.5 | 1.46 |
| Positions | 2 | 13.0 | - |
| Stages x Positions | 4 | 82.5 | 17.93** |
| Replicates | 57 | 2.7 | - |
| Error | 112 | 4.6 | - |
| Total | 179 | | |

** Significant beyond the 1% point.

On the basis of the results presented, there are no significant differences in stomatal size for flag leaves, regardless of the stage of plant development or of the position on

the leaf at which the stomata are measured. The stomata are slightly smaller when the head is just emerging. Flag leaves were never collected at this stage, however. The stomata at the extremities of the leaf appear to be more variable, lending support to the choice of mid-leaf measurements.

III. Experiment to determine whether stomata on various tillers of the same plant differ in size.

In Test 3 particularly, where the plants had tillered profusely, it was often difficult to determine accurately which was the main culm. To get some indication as to whether the flag leaf stomata on the tillers differed in size from those on the main culm, five leaves were taken from the tillers of each of five plants of Red Bobs. For all but the youngest tiller, the spikes were well out of the boot, a stage comparable to that when measurements would normally be made. Only the youngest tiller had smaller stomata. This tiller would never be mistaken for the main culm. It is therefore concluded that if the leaf from a tiller greatly resembling the main culm were taken accidently, no real error would be encountered.

Realizing the danger of basing conclusions on single small tests it is, nevertheless, felt that the exploratory experiments here reported for stage and position are indicative of variations which actually occur. The three leaf stage appears to be most satisfactory for seedling leaf determinations, while a stage when the flag leaf is well out of the boot is best for flag leaf determinations. In either case, a trans-mid-leaf sample has advantages.

# APPENDIX "C"

## A Mass Crossing Test.

## A MASS CROSSING TEST.

Preliminary emasculations in 1940, with subsequent open pollination in buffer rows of Red Bobs, produced seed sets of approximately 50 per cent on the average. Since emasculation may be achieved with relative ease and rapidity, it was thought that a "mass" crossing scheme might produce $F_1$ seed in fairly large quantity. Large $F_1$ populations are highly desirable for various studies, and methods to obtain them have been sought by several workers. Suneson and Riddle (30) have used male sterility to obtain $F_1$ populations for studies on hybrid vigor in barley. The "approach method" described by Rosenquist (27) has been found useful where a large $F_1$ populations of wheat or barley is required. A search through the literature, however, did not reveal any method similar to the one described below.

The same seven varieties described in Part I of this thesis were used in the present investigation. Erythro was chosen as the male or pollen parent because it is easily distinguished. To avoid contamination by foreign pollen, the test was well isolated from other wheat.

The six varieties chosen as female parents, i.e. those to be emasculated, were arranged in six series or replicates. Each variety appeared twice in each series in single rows, 12 feet long and 9 inches apart. A blank space 18 inches wide was left between each pair of rows to facilitate handling. Six plantings of Erythro were made at four day intervals, the rows being between and beside each two rows in a series, thus allow-

ing only a 4½ inch space between male and female parents. Two plantings of Erythro were made before the other varieties were planted. On the date of the third seeding the female parent material for all series was planted together with a planting of Erythro. This method allowed for ample Erythro pollen to be present, regardless of the maturity of the female parent. Erythro was the only variety which was allowed to flower.

Owing to the pressure of other crossing work it became necessary to abandon this method before a maximum amount of seed could be obtained. Early observations on the number of seeds set were not in the least encouraging, but at harvest time the percentage seed set was found to be good. In other words, a test which appeared at one time to be an almost certain failure proved to be a reasonable success. The small amount of seed obtained was grown in separate plots in 1942 and critically examined for "selfs", but none were found, indicating favorable possibilities for the method.

The relative value of such a method of producing large quantities of $F_1$ seed necessarily depends, to a considerable extent, on the amount of natural crossing within the varieties involved. Various workers have studied natural crossing in wheat (15, 20) and barley (26, 29) and the question needs no discussion here.

Allowing for certain difficulties, which might possibly be overcome, the writer is convinced that the mass crossing method herein described warrants further consideration where large $F_1$ populations are desired. It is suggested, however, that the number of varieties should be limited since considerable work is

required at the time of emasculation. The method should be exceedingly valuable where intra-varietal crosses are made, provided reasonable care is taken to assure isolation.

B29751